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NEW LIGHT ON EVOLUTION FROM RESEARCH ON THE GENUS CREPIS[1]

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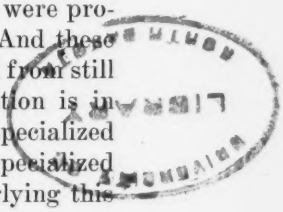
THE theory of organic evolution is now generally accepted by enlightened people. They think of the many kinds of plants and animals which inhabit the earth as having descended from very different ancestors. Botanists believe that all our flowering plants have evolved from simpler forms in which the sexual organs were produced on some vegetative part of the plant. And these flowerless plants are believed to have descended from still simpler forms. The account of animal evolution is in general similar. More complex or more specialized forms have evolved from less complex or less specialized forms. What are the general principles underlying this grand process of organic evolution?



The concept that the many different species of living things now inhabitating the earth have all descended from earlier species, and those from still earlier species, and so on back to the origin of life on the earth is the primary thesis of the theory. This concept is based on two general principles: (1) the continuity of physical life which is made possible in higher plants and animals by sexual reproduction; and (2) the metamorphosis of species—new species arise from pre-existing species.

This second principle was the basis of Charles Darwin's classical theory. Darwin assumed that the evolutionary process, which he termed "descent with modi-

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fication," was made possible by the gradual accumulation of small changes under the influence of natural selection. And natural selection was assumed to operate through the preservation of those individual organisms which were able either to live in a changing environment or to escape from it into a new region where the environment is favorable. In spite of all doubts and attempts to disprove it in the past, this principle of natural selection is recognized to-day as an important factor in organic evolution. But it is only one of several factors. Another is the way or ways by which the individuals comprising a species reproduce themselves; because this too affects the preservation of such new hereditary changes as may occur from time to time. Also of importance is the number of individuals making up the population (or populations) of a species, at least when the number is below a certain optimum. For, in inverse proportion to the population size, there is random elimination of hereditary elements in each generation, because these hereditary elements or genes are shuffled about among the germ cells, and many more germ cells are formed than can function in producing the individuals of the next generation. This in itself tends to produce changes in species.

But all these so-called factors are merely the conditions which determine the preservation of genetic changes in the species. The more basic problem, which was sensed but not solved by Darwin, is to discover the real nature of those hereditary changes which are continually occurring in individuals and which, under favorable conditions, may make possible a new character or quality of the species. Two things, however, Darwin did stress: first, that these changes in individuals, which lead eventually to the origin of new species, are probably small; and second, that modification by descent is a slow, gradual process.

Just the opposite conception, to wit, that new species result from a single drastic change, affecting many parts and functions of the organism, has had its advocates

among biologists, beginning with de Vries in 1901. Very recently this theory has been revived by one of our colleagues on the grounds that true species differ from one another in some more subtle yet profound way than do mere subspecies or varieties; and that new species originate through some sort of "systemic mutation," due perhaps to the alteration of the chromosomes. However, the opposite view, namely, that the differences between species and subspecies are largely matters of degree of differentiation, is accepted by the majority of biologists. And Darwin's original view, that species change gradually into new species through the slow accumulation of small changes, is the prevailing view to-day. The evidence from *Crepis* certainly supports this view, as I shall try to show. But first we need more definite ideas about the nature of those genetic changes which may gradually bring about the transformation of one species into another.

I shall introduce these ideas while introducing you to the group of plants on which I have been working for the past quarter-century. *Crepis* is a large genus, containing 196 species. Only one of these species, the pink-flowered *Crepis rubra,* has become a common garden flower. All the others are wild species, a few of them being weeds. As a group, *Crepis* is closely related to *Lactuca,* which contains the lettuce of our victory gardens, and to *Taraxacum,* which includes the common dandelion and its wild relatives. After bringing together the dried specimens of all these *Crepis* species from various herbaria, I was much impressed by the extraordinary diversity within the group with respect to the size and habit of the plants as well as the form of their roots, leaves, flower heads, and especially their fruits or so-called seeds. These plants, it seemed, must also exhibit great diversity in their life processes, since the various species are peculiarly adapted to extremely different environments, such as swamps, deserts, meadows, seashores and alpine peaks.

In course of time I was able to obtain live seeds or roots of many species of *Crepis;* and this enabled us to make our microscopic studies of their chromosomes. Eventually it was found that most of the species have either 8, 10 or 12 chromosomes in their somatic cells; but three species are known which have only 6. In Fig. 1 are shown camera lucida drawings of one member of each pair of chromosomes found in root tip cells from: *Crepis terglou-*

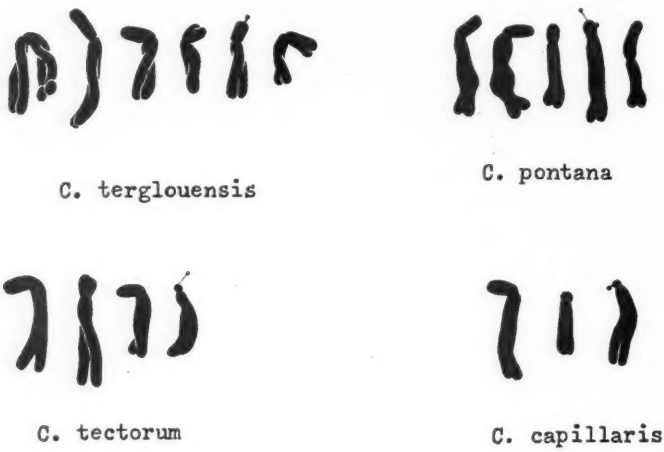

FIG. 1

ensis, a high alpine perennial known only from the European Alps; *Crepis pontana,* another alpine perennial of the European Alps; *Crepis tectorum,* a widespread annual of Asia and Europe; and *Crepis capillaris,* a widespread European annual which has become established as a lawn weed here and there in North America, New Zealand and probably other parts of the world.

Now the chromosomes are found in each of the thousands of tiny cells of which the plant or animal body is composed; they usually exist in pairs and they contain the all-important hereditary elements or genes. A single chromosome may contain hundreds of genes; and since a complete set of genes is essential to normal growth and

development, each individual has the same number of chromosome pairs in all its somatic cells. But, when the germ cells are formed, each cell gets only one member of each pair of chromosomes. Thus each germ cell has one complete set of genes, whereas the fertilized egg and all the body cells contain two doses of each gene, one from each parent.

Up to the present it has been possible to study the chromosomes in 113 species of *Crepis*. Since most of the species have either 12, 10, 8 or 6 chromosomes, that is, 6, 5, 4 or 3 chromosomes in their germ cells, the question arises as to how such a basic series was created. If this could be discovered, it might also be possible to learn whether a change in chromosome number causes changes in form, structure or function in the plant, or in other words, whether the changes in chromosome number which occurred during the evolution of these *Crepis* species have any causal relation to the changes in the morphology and physiology of the plants. Since the changes in chromosome number, which created the series, 6, 5, 4, 3, must involve the loss or addition of a single chromosome from the basic set, it would appear that such changes might be merely mechanical in nature. Does the origin of new species depend primarily upon such changes in chromosome number or upon some more fundamental type of genetic change such as gene mutation?

And what, you may ask, is gene mutation? Also if genes change how does one account for hereditary resemblance and the stability of many species? The answer to the second question is that genes are actually stable entities and yet they are so constructed as to be capable of an occasional change. To express one's concept of gene mutation one must first have a concept of a gene.

A gene may be thought of as a molecule or part of a molecule and a gene mutation as a molecular change of some sort at a definite point in a particular chromosome. The chromosomes are known to contain organic molecules so complex in structure that the number of possible per-

mutations and combinations of changes by loss, addition or substitution of small groups of atoms at different points is well-nigh infinite. Hence it is conceivable that, sooner or later, any gene may undergo a change. And, since there are hundreds of genes in one set of chromosomes, and thousands of germ cells each with that same set of chromosomes, there would seem to be a good chance that some single gene in some particular germ cell might mutate. As a matter of fact geneticists have learned by experiments that gene mutations actually do occur at different rates in different genes and under different conditions. Some genes change rarely, others more frequently, and still others very frequently under comparable conditions.

Now gene mutations are recognized by some geneticists as being of two general categories which may be designated as major or primary and minor or modifying, though the distinction can not be clear-cut, because some mutations are border-line cases. It should be emphasized that what we are actually describing when we use these terms, major and minor, or primary and modifying, is the observed effects of the gene change, not the gene itself.

A major gene change so influences the development of the individual as to cause easily observable changes, either morphological or physiological or both. These changes range from differences in size, shape or function of parts up to monstrosities or even to lethal effects. For example, in *Crepis tectorum* some perfectly normal plants possess an interspecific lethal gene in double dose. When such a plant is crossed with another species, *Crepis capillaris,* plenty of hybrid seeds are produced but all the young seedlings die. Other *tectorum* plants have one lethal gene and one normal partner of that gene. Such a plant, crossed with *C. capillaris,* produces plenty of seedlings but half of them will die. Still other *tectorum* plants have the two normal partners of the lethal gene, and their offspring from crossing with *C. capillaris* will

all live and will develop and produce flowers. Thus the gene-mutation that produced this interspecific lethal is clearly a major change.

In another species, *Crepis foetida*, there exists a gene difference which affects only the shape of the juvenile leaves. After the plants develop beyond the early rosette stage their juvenile leaves disappear and they can not be classified according to the character mentioned. Now the mutation which caused this gene difference is really on the border line between the major and minor categories.

The strictly minor mutations actually cause such small changes that they can be detected with difficulty if at all. And yet, by careful selection experiments, like Castle's famous research with modifying genes in hooded rats and Whiting's recent discovery of modifying genes affecting sex in a parasitic wasp, it has been shown that these minor genes operate together in series and thereby profoundly affect adult characteristics. One such minor mutation may not be notable to an observer, but when it has been recombined with other genes or with more modifiers of a similar nature, the results will provide material for the effective operation of selection. Thus it is possible for a species population to undergo a gradual change in its characteristics through the birth of certain individuals which possess new minor mutations. Furthermore, the combined effects of fortunate combinations of genes may gradually bring about important changes in some part of the species population. It only remains for this changed segment of the population to become separated from the rest through migration or by possible environmental change or by some internal change within the plant, making reproduction with the original type of the species impossible, to have the stage set for the origin of a new species.

One may ask, therefore, what have been the roles played by gene mutations on one hand, and by changes in chromosome number on the other hand, in organic evolution?

To this fundamental question the research on *Crepis* has revealed some definite answers which I shall present toward the close of the lecture.

Before reaching the vantage point from which such generalizations could be made, it was necessary to arrange the species of *Crepis* in sections such that the members of each subgroup are more closely related to one another than to the members of any other section. In classifying the species into subgroups, my constant aim has been to arrange both the sections and the species in each section in their probable phylogenetic sequence. By this is meant an arrangement representing, as nearly as possible in a linear series, an orderly progression from the oldest or most primitive species to the youngest or most advanced species. At this point let me anticipate the presentation of the evidence to say, this evidence will show that there is an actual difference, and a great difference too, in the comparative length of time that the most primitive and most advanced species have been in existence. Therefore, we are actually warranted in calling them the oldest and youngest species in the genus. In other words, no matter how different the youngest species may look from the oldest ones in the series, our evidence shows that they have descended from those oldest species, or similar ones that are now extinct, through a long line of interconnecting forms.

The hazards of phylogenetic speculation are well known to biologists. But most such speculations in the past have been based largely on evidence obtained from a single biological discipline—most often from morphology alone, or from morphology supplemented by anatomy. For this reason I have based my phylogenetic classification on as broad a foundation as possible by obtaining and synthesizing evidence from several different disciplines, all for the purpose of determining the true relationships between the species. Although my first classification was made on the basis of morphology, it has been checked and rechecked against the evidence from the

chromosomes, from experiments with hybrids, from geographic distribution and from any other evidence available.

The morphological criteria of phyletic relationship need not be discussed in detail here. Briefly, it was found that the most primitive species in the genera are robust, leafy perennials with few large flower heads in which the involucre consists of many large scales or bracts that remain unchanged as the fruits ripen. The individual florets and fruits or achenes are also comparatively large; and the achenes are not highly specialized for distribution of the seeds by the wind. In marked contrast, the most advanced species are slender annuals with a basal rosette of leaves and nearly naked stems, numerous very small flower heads in which the involucre consists of a few small bracts that become thickened and reflexed as the fruits ripen. The individual florets and fruits or achenes are very small; and the achenes are highly specialized for wind distribution by the presence of a long slender beak which bears the fine pappus bristles like a parachute at its summit. All the other species in the genus fall into subgroups which form a connecting series between the two extremes.

The chromosomes have provided some valuable evidence on phyletic relations in *Crepis*. When we compare the karyotypes with longest and shortest chromosomes in each of the four number classes, 6, 5, 4, 3, we find that we have selected a more primitive and a more advanced species in each case. There is in fact a definite tendency in this genus for the younger species to have shorter chromosomes. There is also a tendency for the chromosomes to be more asymmetrical in the more advanced species. These are interesting trends, but they are merely coincidental. The most important phenomenon for the present discussion is the progressive reduction in chromosome number from 6 to 5 to 4 to 3, since the majority of the species in the genus belong in this series. I might add that there are a few species of *Crepis* with

other chromosome numbers. For example, there is one section having the germ cell number 7 and one in which it is 11 or some multiple of 11. But these are subsidiary groups with special problems as to their origin. They are side issues from the main line of events in the evolution of the genus.

Statistical analysis has revealed two very important trends in the evolution of this genus. (1) There is strong positive correlation between phylogenetic position and chromosome numbers. On morphological grounds, sections I—V contain the most primitive species in the genus and the majority of these species have 6 chromosomes in their germ cells. On the same basis sections XIX—XXVII contain the most advanced species in the genus and the great majority of these have 4 or 3 chromosomes in their germ cells. In the intermediate sections the chromosome numbers are about equally divided between 5 and 4. (2) There is also strong positive correlation between phylogenetic position and length of life of the individual plant. In the primitive sections the plants are all perennials; in the most advanced sections they are mostly annuals, and the most advanced species are the shortest lived of all the annuals. Thus it is clear that reduction in chromosome number and shortening of the life cycle have both gone along with morphological reduction and specialization. And we are assured of consistency in the phyletic evidence from the first three fields, morphology, physiology and cytology.

Now the evidence from genetics and cytogenetics is also consistent with all the other evidence. The interspecific lethal in *Crepis tectorum*, illustrates a major gene difference; and the two types of juvenile leaves in *Crepis foetida* were mentioned as a borderline case approaching the minor category of gene differences. In several of our artificial crosses between species having the same chromosome number, we have obtained data showing that the two species differ in numerous minor gene differences affecting the size and shape of various parts of the plant.

From this we infer that these species have diverged from a common ancestor through the accumulation of minor gene mutations. This is one important contribution from the genetic studies.

Another contribution from genetic research is found by summarizing the results of 170 different crosses between *Crepis* species. The most significant thing about these data is the support they give to the arrangement of the species in their sections. These attempts to obtain artificial hybrids were made over a period of 25 years and the choice of parents was determined by the species available at the time. There are two types of crosses, intrasectional and intersectional. In the first type the species crossed were always in the same section and eight sections are represented in these experiments. In the second type the two species crossed were always in different sections and 17 of the 27 sections are represented in these experiments. There were 43 crosses of the first type and of these only 7 per cent. failed while 93 per cent. gave hybrids. Over 80 per cent. of these hybrids were vigorous plants and a third of these were fairly fertile also; whereas only 17 per cent. were weak and sterile. Of the second type, intersectional crosses, 127 were attempted, and of these 40 per cent. failed and only 60 per cent. produced hybrids. Of these hybrids only 60 per cent. were vigorous and none were fairly fertile, whereas all were nearly sterile and 40 per cent. were very weak plants. This evidence clearly indicates that the sections represented in these experimental crosses are groups of species that are more closely related to one another than to the species of other sections. To this extent it strongly supports the sectional scheme of classification which was worked out on a morphological basis.

Two contributions from cytogenetics will be presented because of their important bearing on organic evolution. The first is the work of a Russian worker. By treating seeds with x-rays, examining the chromosomes of the seedlings, and practising adequate breeding technique,

Miss Gerassimova eventually obtained a plant of *Crepis tectorum* which still had all the chromosome material present and which looked just like the original plant. But pieces of the chromosomes had been interchanged between different pairs so that the new type, *Crepis nova* has two long V-shaped pairs and two very short pairs (note shape of chromosomes in normal *C. tectorum,* Fig. 1). This new chromosome type not only looks externally like other *tectorum* plants but it is equally fruitful when self pollinated. Yet, when it is crossed with the original, normal *tectorum* type, the hybrids are as highly sterile as the hybrids between many true species. Thus *Crepis nova* is sexually isolated from normal *tectorum* plants. And, as Miss Gerassimova points out, the sexual isolation of two parts of the same population makes possible their gradual differentiation by means of gene mutations. These may change an incipient species like *Crepis nova* more and more in size, shape and function of parts, even under similar environmental conditions, and at the same time, may increase its sexual isolation from its ancestor. Now the interchange of parts between different chromosome pairs was caused by the x-rays used in this experiment. But the same sort of mechanical changes also occur in nature. Though their cause or causes are as yet unknown, it is clear that such interchanges provide the first step in the reduction in chromosome number from 4 to 3, or 5 to 4, etc., as will be shown in the next contribution.

This is the research of Dr. Hassan Tobgy (1943), one of the Egyptian students who worked in our laboratories. He crossed *Crepis neglecta* with *C. fuliginosa* and made an intensive study of chromosome behavior in the hybrids. In Fig. 2, on the right is *C. neglecta,* and on the left *C. fuliginosa,* with reciprocal hybrids between, which look just alike. These hybrids were extremely sterile, producing almost no good seed, even though the two parent species are very closely related. This sterility of the hybrids is caused by the chromosome differences in the two species.

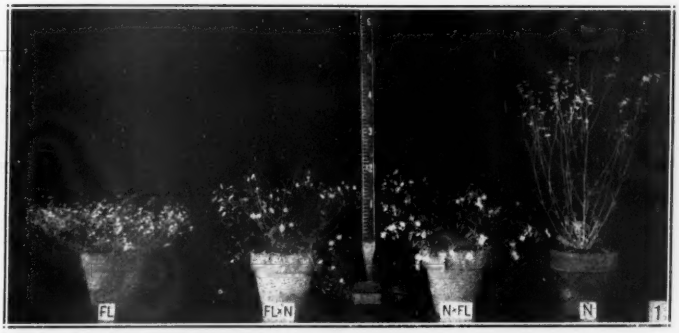

FIG. 2

In Fig. 3, at the upper left, are shown the 3 chromosomes in a germ cell of *Crepis fuliginosa,* labeled A_F, B_F, D_F. There are, of course, two A's, two B's and two D's in each somatic cell and in each spore mother cell. At the upper right are shown the 4 germ cell chromosomes of *Crepis neglecta,* A_N, B_N, C_N and D_N. You will note that the *neglecta* chromosomes are definitely wider than the *fuliginosa* chromosomes, so that in the hybrid set it is

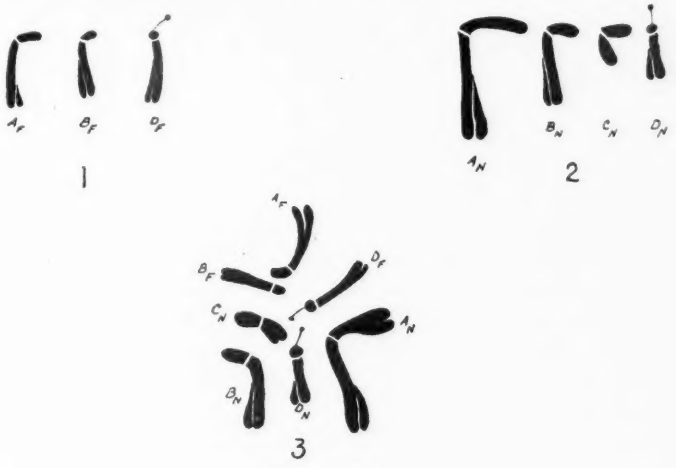

FIG. 3

easy to see that the 3 upper ones are the *fuliginosa* A, B and D and the others are the 4 *neglecta* chromosomes.

In *Crepis fuliginosa*, when a pollen mother cell is about to go through the reduction division, (Fig. 4, upper left) the two A chromosomes come together, also the two B's and the two D's, the latter being always associated with the nucleolus at this stage. Then (2) as the pollen mother cell (the surrounding wall of which is not shown) begins

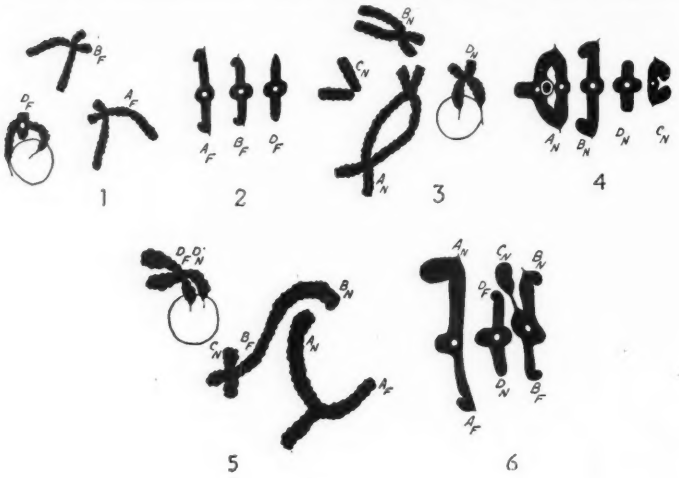

FIG. 4

to divide, the 3 pairs of chromosomes orient themselves so that one A will go into one germ cell and the other A into another. Similarly with the two B's and the two D's. In the same way a pollen mother cell of *Crepis neglecta* has 4 pairs; and in the reduction division the members of each pair are separated into different cells (3, 4). Now let us compare these same stages in the hybrid. We find (5) a pair of A's, a pair of D's, and an association of three chromosomes, *neglecta* B, *fuliginosa* B, and *neglecta* C. Then, in division of the pollen mother cell (6), the two A's and the two D's are separated, while the B and C of *neglecta* are separated from the B of *fuliginosa*.

From a great deal of evidence like this, but still more precise, Tobgy was able to show conclusively that the B chromosome of *Crepis fuliginosa* contains the essential hereditary elements of both the A and C chromosomes of *Crepis neglecta*. Therefore, the 3-chromosome species *fuliginosa* either originated directly from *neglecta,* or the two species arose from a common ancester, with 4 pairs of chromosomes. This cytogenetic evidence that a 3-chromosome species descended from a 4-chromosome species is of basic importance because it corroborates our other evidence on phylogeny in *Crepis*. Furthermore, we have similar evidence from the research of Marta Sherman Walters (1944) that a certain 4-chromosome species descended from a 5-chromosome ancestor.

We have examined some of the evidence on phylogeny in *Crepis* coming from comparative morphology, physiology, genetics and cytogenetics. Before attempting to describe the origin and development of this genus, it is necessary to consider the evidence from geographic distribution. All the evidence presented thus far agrees with the assumption that *Crepis* is monophyletic, that is, that the 196 species in this genus have descended from one ancestor, or from a small group of very closely related species, and therefore that there was one geographic center of origin. A study of geographic distribution aims to discover that center of origin and the principal migration routes followed in reaching the present world wide distribution of the genus.

The best evidence on center of origin is found by comparing the distribution of the older and younger species in each section. When this has been done it becomes clear that the distributional evidence from all the sections is consistent in pointing to north central Asia as the center of origin. A few sections will serve as illustrations.

In section 4, the older species are on opposite sides of Eurasia, three of them in the mountains of southern Europe, while the fourth is in northern Japan. The four younger species are nearer the assumed center of origin.

In section 6 all four species are primitive and they all occur in the Pyrenees, Alps and Balkan Mountains. But one of them, *C. conyzaefolia,* also has a disrupted distribution extending clear to the Altai Mountains, which is in the assumed center of origin. Hence this is a guiding species, having left behind some remnants marking its route of migration from north central Asia.

Section 12 contains seven species which are mostly in south central Asia. But *Crepis nana* also extends through the mountains of central Asia and Siberia into Alaska, arctic Canada, and south through the Rocky Mountains, and the Sierra Nevada. The seventh species, *Crepis elegans,* was obviously derived from *Crepis nana,* and it occurs only in North America. The distribution of this group is important in helping to establish the antiquity of *Crepis.* The center of origin for this section is evidently central Asia. Some at least of the isolated stations for *C. nana,* located in eastern North America, are on unglaciated islands in a heavily glaciated region. This certainly indicates that this species migrated from Asia into America before the Ice Age.

Section 21 is especially interesting. Two of the four species are in the Chinese-Tibetan Mountains. Another occurs in northeastern Siberia. The fourth, *Crepis multicaulis,* is most advanced and is a polymorphic species. It extends from the western Himalayas and Pamirs to the Altai; also it exists today on a small, probably unglaciated area in Varangar, the extreme northern end of Norway. Central Asia is surely indicated as the center of origin and it is probable that *C. multicaulis* was widespread in northern Europe before the Ice Age but was almost completely wiped out by Pleistocene glaciation.

Now we can safely generalize as follows: Assuming central Asia to be the center of origin for *Crepis,* we find general agreement in the geopraphic distribution of the various sections; and in certain sections we find striking conformity with a well-known principle of paleon-

tology—Matthew's Principle—which states that, in groups of related species living at a given time, the most primitive will be found farthest from the center of origin. While numerous exceptions and modifications to this principle are known, it still holds generally for many groups of higher organisms. The conformity with Matthew's Principle which we find in *Crepis* strengthens our assumption that central Asia is the center of origin for this genus.

We can now turn our attention to the migrations of *Crepis* species away from the center of origin. But, in order to consider this problem intelligently, we must first consider the background of earth history and the antiquity of *Crepis*.

The background of earth history must be considered at least as far back as the Mesozoic era because it will be pertinent to inquire whether north central Asia has been continuously a continent since that era or even longer. If so, then not only *Crepis* and its immediate ancestors but its much more remote ancestors, extending back to the earliest forms of flowering plants and their ancestors, could have developed in that same region. This point will be mentioned again. As for the genus *Crepis*, we are concerned only with the Cenozoic era and, particularly in the Tertiary period, with the Miocene and Pliocene epochs; and in the Quaternary Period with the Pleistocene epoch which includes the Ice Age. The flowering plants as a group originated during the period preceding the Tertiary period. But, as we shall see, *Crepis* probably originated about the middle of the Tertiary period in early Miocene or late Oligocene.

Concerning the antiquity of *Crepis*, the distributional evidence alone is convincing. The map (Fig. 5) shows the present distribution of the genus. The numbers indicate sections. Without going into details, only three points need emphasis. (1) Sections 4 and 6 contain some of the oldest species in the genus and some of these are now found only at very high elevations in the European Alps.

These heights were covered with ice during the Pleistocene epoch; and European botanists agree that these alpine plants must have moved up onto the peaks from surrounding areas gradually as the ice disappeared. This means of course that they were already in that

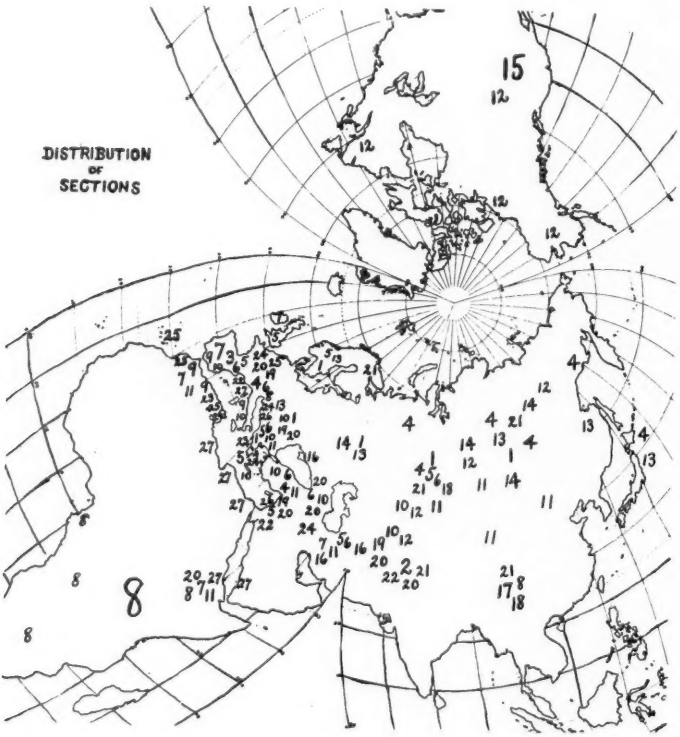

FIG. 5

region at least as early as the Pliocene epoch. (2) The present occurrence of *Crepis nana* on small unglaciated areas in Newfoundland indicates that *Crepis* had a pre-Pleistocene origin; and the same reasoning applies to the isolated population of *Crepis multicaulis* in northern Norway. (3) Our study of the American species led

Stebbins and myself (1938) to the conclusion that some of them or their ancestors must have migrated from Asia to America in the Miocene epoch.

The deductions from distributional evidence have been well substantiated by the discovery of some fossil seeds. These fossils were identified as three different species of *Crepis* by European botanists; and, from the excellent lithographs published by Reid and Reid (1916), I am satisfied as to their identity. In fact they are easily matched with seeds of the following present day species: *Crepis terglouensis*, a primitive relic species of the high Alps, having 12 chromosomes; *C. mollis*, another 12-chromosome species, but less primitive than the preceding and more wide spread; and *C. conyzaefolia*, the most primitive of all the 8-chromosome species. The last is the guiding species mentioned earlier. These fossils were found in Middle Pliocene clay pits, the Reuver plant beds on the Dutch-German border. In Tertiary times this area was in the huge delta of the Rhine River, which must have transported the seeds from the uplands. The point to be emphasized here is this: If these plants had already migrated from Central Asia, an air-line distance of over 6000 kilometers (3,700 miles), they must have had their origin much earlier than the Pliocene epoch. This agrees with the conclusions derived from present-day distribution, especially of the American species, that *Crepis* must have originated not later than early Miocene.

Having determined the center of origin and the period in the earth's history when *Crepis* originated, we shall turn in a moment to the story of the origin and development of this group of plants. Before doing so it should be made clear that great care has been taken to ascertain that this hypothetical account of *Crepis* is consistent with the facts and accepted hypotheses of geology, paleontology and floristics. Space forbids an account of this evidence here—it is thoroughly reviewed in the monograph on this genus. The summary statement can be made, that both *Crepis* and its more and more ancient

ancestors all could have developed in north central Asia, since the land area from the Altai Mountains to Kamtchátka has been a mountainous continent ever since the Paleozoic era. Also the present continental outlines were established, for the most part, before the middle of the Tertiary period; and the great southern mountain systems from the Himalayas to the Pyrenees, were developing during the Tertiary and Quaternary periods. Lastly, but equally important, Asia was connected with North America and with Europe by continuous land throughout the Miocene, Pliocene and Pleistocene epochs, and with Africa during the Miocene at least. These land bridges were doubtless the migration routes followed in establishing the present world wide distribution of *Crepis*.

Originating presumably in the Altai or eastern Tien-Shan Mountains, the earliest species of *Crepis* probably migrated from the humid areas at lower elevations upward onto the drier steppes, while some of them eventually reached alpine elevations, becoming gradually differentiated in form and structure as they became adapted to more and more diverse environments. During this earliest period of development there must have been a tendency for those species to radiate in all directions. But differences in the environments to which various species had already become adapted would largely determine the directions in which they could migrate most easily. Thus the moisture-loving, lowland species of sections 1 and 5 moved a little northeastward but mostly westward or southwestward; whereas the alpine species of sections 4 and 11 probably jumped along the mountain tops northeastward and eastward as well as southwestward into southern Europe. The alpine *Crepis nana* of section 12 found its way along the mountains into arctic North America; and the same general route, but at lower levels, was taken by the ancestors of section 15. In section 13 one species, the oldest, got as far east as Japan, the next oldest spread from Manchuria to western Europe, and in southern Europe it gave rise to the most advanced member of this section. In section 21, one

species got to northeast Asia, two species, along with representatives of sections 8, 17, and 18, moved into southeast Asia, while the fourth species, *C. multicaulis*, spread through south central Asia and westward across Russia to northern Norway where it exists today. All the other species in the genus, or their ancestors, either remained in central Asia (and a few did so) or they took the southwesterly route which brought them eventually into Africa, Asia Minor and the Mediterranean region, where the greatest number of new species have evolved (see Fig. 5).

In bringing this lecture to a close, I should like to discuss briefly the general aspects of evolution in *Crepis*. Three general conditions and three vital processes have been important in the evolution of some 200 species from a few original ones. The first condition is secular. As a rough estimate, the duration of time from early Miocene to the present is probably something like 20 to 30 million years. Although many *Crepis* species are perennial, all of them produce new seed progeny each year. Contemplating 20 to 30 million generations of *Crepis* plants, with a certain chance of successful new types occurring in any generation, one begins to visualize the possibilities for evolution. Furthermore, during this tremendous span of years, the earth has passed through three geological epochs and begun a fourth. Each of these epochs brought gradual but profound changes in environment to which the terrestrial plants had to adapt themselves, or escape by migration, or be wiped out.

The second condition then is environmental change. There are three most important groups of environmental changes. (1) The cooling and drying of the climate in the late Miocene and Pliocene epochs; this induced the general southward trend of migration. (2) The processes of mountain building that recurred from time to time throughout the life of *Crepis* in Southern Eurasia from the Sino-Himalayan region to the Alps, the Pyrenees and the Grand Atlas. These mountain-building processes opened new migration routes for some species

and erected barriers for others. The importance of this environmental feature is shown by the fact that sixty per cent. of the endemic species of *Crepis* occur in these mountains, including those of Iran, Asia Minor and the Balkan Peninsula. (3) The effects of glaciation in the Pleistocene epoch, including extreme vacillation in temperature and moisture, especially in the Mediterranean region. It is in the Mediterranean region that we find the greatest concentration of younger species.

The third condition is isolation, which may be accomplished in two ways. Firstly, we note the effect of migration of species which may result eventually in the isolation of populations. Migration may be either altitudinal or horizontal. In either case it makes possible a separation of two or more populations of any one species together with the selective effects of the changed environments into which these populations have moved. Secondly, we recognize the creation of isolation between groups of individuals within any one species by means of genetic changes taking place within the plants themselves. Those mechanical changes in the chromosomes, which led up to reductions in chromosome number from 6 to 5, to 4, to 3, are an effective internal mechanism making for isolation. And, when a change in chromosome number has been finally accomplished, a very effective barrier to the production of fertile offspring has been set up. At an early stage in this speciation process the two new types with different chromosome numbers are not likely to differ at all in external appearance or in normal fertility. This important fact was clearly demonstrated by Miss Gerassimova in her interesting experiment with *Crepis tectorum*. It has also been demonstrated by Dubinin, another Russian, working with the common fruit-fly, *Drosophila melanogaster*, which normally has 4 pairs of chromosomes. Dubinin's new 3-paired form of this fly, which resulted from x-ray experiments, still looks like the normal 4-paired form, but hybrids between the two forms are more or less sterile. Dubinin has proved that the reduction from 4 to 3 pairs of chromosomes in this experi-

ment was accomplished by means of chromosomal interchanges.

Thus we see that the third condition and the first vital process both accomplish the same essential step in the origin of species. The third condition involves the spatial separation of different populations of the same species. The first vital process involves the sexual isolation of different parts of the same population by the creation of an internal mechanism which is capable of becoming more and more complicated and effective as time goes on.

The second vital process is differentiation between isolated populations. In *Crepis* this has been accomplished largely by means of minor gene mutations. It matters little how two parts of the same species become isolated. Whether the separation be spatial or due to an internal mechanism, the recurrence of gene mutations is potentially able to create endless changes in the form and function of the plant and its parts. Some of this differentiation may be non-adaptive. But when natural selection is operating it will tend to be adaptive. Our own research on the genetics of hybrids has shown that gene mutations have certainly brought about the present great diversity of *Crepis* species within the several chromosome number classes, 6, 5, 4 and 3.

The third vital process is adaptation through gene mutation and natural selection. There are several important special adaptations in *Crepis*. One of most profound significance in the evolution of this genus is the change in type of root from the rhizome to the deep taproot. This made it possible for perennial plants to maintain themselves under drier conditions than the oldest species in the genus could endure. From these first deep-rooted perennials many more advanced perennials and all the biennials and annuals have descended. The reduction in length of the life-cycle is another adaptation to xeric conditions which, as we have seen, is correlated with progressive evolution in this genus. This reduction trend has reached its peak in the small, delicate, desert

annuals. These plants are specialized for desert conditions not only by their small size, but also by their extreme precocity (they produce flowers and fruits within a few weeks after germination of the seed) and by the longevity of their tiny seeds. Seeds of *Crepis senecioides,* the most advanced type in the whole genus, will germinate after four years or more in storage, whereas seeds of many perennial species will die within one or two years. Special adaptations for distribution of the seeds by the wind are very striking in *Crepis,* particularly the specialized involucre and the development of a long, fine beak on the slender seeds of the most advanced species. Various other special adaptations are found in *Crepis* species.

Now all these specialized types have close relatives which are not so highly specialized and which flourish under less rigorous conditions. The most extreme adaptations in the genus are still connected, through a long series of more and more primitive species, with the oldest members of the genus and their nearest ancestors. Furthermore, our genetic research on many interspecific hybrids has shown that the species crossed differ in numerous genes. In fact the net result of all this research leads to the conclusion that there is no reason to doubt and many reasons to believe that the basic cause of all this evolution through adaptation is gene mutation. The processes of differentiation and adaptation have been slow and gradual. Minor changes in genes have probably caused most of the differences between individuals which have made these adaptations possible. But, with 20 to 30 million generations and millions of plants in each generation, together with changing environments and isolation of populations, there was adequate opportunity for the production of those occasional favorable mutations and of subsequent new combinations of genes which were required for progressive development. All through this long, slow process, the guiding principle which eliminated the unadapted and preserved the adapted individuals must have been none other than natural selection.

We have found that the evolution of *Crepis* rests on three conditions, namely, plenty of time; plenty of environmental changes with the passage of time; and isolation of populations through migration; and on three vital processes: (1) the creation of isolation through changes in chromosome numbers and associated genetic changes; (2) differentiation of species within the several chromosome number groups by means of gene mutations; (3) along with differentiation, adaptation through gene mutation and natural selection.

In answer to the fundamental questions with which we started, we can state with assurance that changes in chromosome number, and the attendant changes in chromosome structure, have been important in creating isolation between groups of individuals within a species; and that these structural changes probably account for the arithmetical series of chromosome numbers found in many genera of animals and plants; but that they have not been important in creating the morphological and physiological differences between species. This differentiation process in the origin of species, we have found, is made possible by the accumulation of gene mutations occurring in already isolated groups or populations.

These two conclusions are in general agreement with most other recent investigations in this field. They are diametrically opposed to the hypothesis of speciation by sudden, profound changes in species. At the same time they contribute to a still broader and firmer foundation for the neo-Darwinian theory of evolution.

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A SUMMARY OF EVIDENCE IN FAVOR OF THE TRACTION FIBER IN MITOSIS

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EVIDENCE has accumulated to the extent that a convincing case can be presented for the theory that chromosomes move during anaphase through the agency of an attached body, the traction fiber. The salient points are included here without any attempt at a historical survey.

EXISTENCE OF FIBERS IN THE LIVING SPINDLE

The occasional reports of spindle fibers seen in living cells do not convince opponents denying their visibility. Striae originating in protoplasmic currents or mitochondrial alignment or the nonhomology of mitotic structure in primitive forms are the alternative explanations offered for the fibrillate appearance (*cf.* Martens, 1930). The living fibers found by Cooper (1941) in the remarkable mitoses of grass-mite blastomeres would probably also be rejected as atypical.

There is a hint of fibrillation in ultraviolet photographs of living spindles (Wyckoff, 1934), but with ordinary light the living spindle appears structureless in nearly all living cells. In such cells, fibers can be made to appear by application of acid (Lewis, 1923), but mitosis is checked until the acid is removed. The constancy of fibrillation in the fixed spindle is good evidence for the almost universal occurrence of a fundamental fibrillar structure of the spindle, but since lines of stress can be made to appear in obviously unorganized materials under a variety of conditions, this evidence requires some reinforcement.

Perhaps the best evidence that spindles are fibrillate previous to contact with fixative comes from experiments with centrifugation (Schrader, 1934) and hypertonicity (Bělař, 1929). Spindles distorted by these agents show

upon fixation a fibrillation following the curved axis of the spindle, regardless of the shape it may have assumed. Nor can it be that these agents have of themselves produced a fibrillate coagulation before the distortion, inasmuch as anaphase movement will continue after centrifugation.

Polarized light supplies conclusive evidence that the fundamental structure of the living spindle is fibrillar. Its birefringence is that of a body with longitudinally arranged micellae (Schmidt, 1939; Schmitt, 1939).

This demonstration of the fibrillar structure of the spindle nevertheless does not prove that an individual fiber moves each chromosome. It shows that the necessary entities exist, but they can equally well be called lines of force, lines of flow, or tubes, or even be discounted as bodies without any functional relationship to karyokinesis. Other sources supply us with evidence of fiber participation as against other mechanisms.

Autonomy of Chromosome Movement

We can immediately eliminate some commonly held hypotheses of the relationship between chromosome and spindle fiber if we consider the behavior of the kinetochore and the independent movement of individual chromosomes. Theories assuming the attraction of the chromosome as a whole, as by an electric charge, or transportation of a passive chromosome in the protoplasm (expanding spindle, currents, shifting viscosity zones, pulsating centrioles) are not consistent with certain phenomena of general occurrence. One is the precession of the kinetochore. Division figures show the kinetochore typically in the lead, and the arms trailing to form the typical V-shape of a centrally attached chromosome. That the kinetochore is actually pulling the chromosome is clearly substantiated by fragmenting the chromosome with x-rays. Acentric fragments move irregularly if at all, and dicentric chromosomes are pulled in two during anaphase. Schaede (1929), favoring the passive carry-

ing of the chromosome, cleverly counters by suggesting that the daughter chromosomes first separate at the kinetochore, thereby allowing that portion to be first pulled toward the poles by the anaphase currents. This, however, is not in keeping with the behavior of irradiation fragments, nor with colchicine mitoses, in which the kinetochores are the last part of the chromosomes to separate once the spindle has been inactivated (Hawkes, 1942).

The other principal obstacle the theories of passive transportation must surmount is the individual movement of chromosomes. The anaphase groups do not migrate as if carried in some general drift of the substrate, but rather move at different rates, start at different times, or even pass each other going in opposite directions. This latter is seen in elongate root cells, or flattened animal cells in tissue culture, following the diagonal orientation of the metaphase plate, and is particularly striking in the crowded mitoses of pollen tubes (Sax and O'Mara, 1941). Autonomy of the chromosomes is undeniably in operation during the elimination of paternal chromosomes in the first spermatocyte of Sciara (Metz, 1936). Here, upon a monocentric mitotic figure, the maternal chromosomes move toward the aster while the paternal chromosomes (with the exception of the limited chromosome) move away from the aster center. Chromosome elimination occurs in others of the fungus flies, and autonomy is not restricted to special organisms. As a general rule, the X chromosome in the heterogametic sex precedes or follows the autosomes. So varied and astonishing are the peculiarities individual chromosomes exhibit in their movements that one can gladly agree with Dr. A. F. Huettner's felicitous characterization, "Chromosomes have sense."

This individuality of chromosome behavior, along with the purposeful functioning of the kinetochore, reveals that between the kinetochore of the chromosome and the pole of the spindle there is a pull which can act selectively

on different chromosomes. This eliminates the possibility that the chromosomes are carried in a group by some general change in the cytoplasm, whether this be a current, an expansion of the spindle (phragmoplast), or a progression of zones of gelation. It rules out also the simpler electrostatic theories, in which all chromosomes develop simultaneously a charge over their entire surfaces and move by repulsion and attraction.

Remaining Possibilities

This leaves five theory groups which allow for determination of movement by the individual chromosome, in that the initial stimulus can presumably originate in the chromosome. (1) Movement of the chromosome by surface tension differences. (2) An attractive force between kinetochore and spindle pole. (3) Repulsion between daughter kinetochores of each pair. (4) Pushing apart of the daughter kinetochores by an individual "phragmoplast" for each pair. (5) Spindle fiber contraction. We omit ameboid movement, which has sometimes been invoked to explain chromosome movement, although it is an empty term inasmuch as the chromosomes show no pseudopod formation and none of the gel-sol shifts which are involved in true ameboid movement.

Further evidence from centrifugation can eliminate the first three theories. Shimamura (1940) has shown that in a lily pollen mother cell division figure strongly centrifuged ($5{,}000 \times g$) parallel to the axis of the spindle, the centripetal chromosomes, still held immovably at the kinetochore, form closed V's with the arm considerably stretched. Such a distortion could be interpreted as resulting from marked differences in specific gravity between the central and terminal portions of the chromosome except that centrifugation at right angles to the spindle gives a different alteration of the chromosome. It does not rotate around its own center of gravity, but rather swings around the spindle pole, at some distance from the pole, like a pendulum bob. With ultracentri-

fuging the results are even more striking. Centrifuging chick embryonic cells at 150,000 × g, Beams and King (1936) were able to tear parts of chromosomes completely away from the spindle, leaving only fragments attached to the spindle halves. These halves had swung as separate entities, so that the chromosomes hung free of any support save the centrifugally directed torn surface of the spindle halves. Gelation of the spindle as a result of extreme centrifugation does not explain the rigid support because parts of the chromosome within the spindle, but not attached to the fiber, were displaced centrifugally.

Shimamura establishes the point that the impression one consistently receives is of a material link between kinetochore and spindle pole, this bond being free to rotate about the pole except for some resistance of the viscous spindle, but not easily stretched. His point is well made, but Schaede (1930) interestingly enough, faced with his own evidence as to the unyielding attachment of the chromosome, concluded *a priori* that a traction fiber would be too fragile to hold the heavy chromosome.

So we are forced to resort to more than a common-sense argument. Consideration of the forces involved gives a more convincing picture. Centrifugation results show that the chromosomes are connected to the pole by a force or structure with a strength greater than that which will distort a chromosome. This is revealed in another manner by dicentric chromosomes (McClintock, 1941, and many x-radiation experiments), which are pulled apart during anaphase. The tensile strength of a chromosome can not as yet be stated in dynes, but its retention of a structural identity through millions of cell generations weighs against any easy frangibility, and one obtains from microdissection the impression that a chromosome is held together by forces considerably beyond the order of magnitude of surface tensions acting on minute bodies. For surface tension to supply the requisite force, we must require the cellular interfacial forces of very limited magnitude to act on one side only

of the minute kinetochore, which over its entire surface could not probably develop a force in excess of a thousandth of a dyne. A mathematical comparison of known cellular interfacial tensions with the forces exerted on a centrifuged chromosome would supply the most satisfactory answer to the question of surface tension efficacy. The force on the chromosome can be estimated only when its specific gravity is known, and with further centrifugation experiments and recently developed methods of isolating chromosomes, such data will perhaps become available soon.

Another consideration argues against surface tension and more particularly against an attracting or repelling force acting between kinetochores or between kinetochore and spindle pole. A force strong enough to distort and fragment chromosomes should pull them with more speed than is shown in normal anaphase migration. If we try to explain the slowness as resulting from resistance of the viscous spindle, then we have a situation exactly equivalent to Beams' and King's and Shimamura's centrifugation conditions: opposing forces pulling on different parts of the chromosome. If the spindle retards the arms of the chromosomes with force sufficient to oppose the pull on the kinetochore, stretching of the chromosome should result in normal anaphase, whereas actually we know no such distortion occurs.

In yet another way the concept of an attractive force is incompatible with the dynamics of anaphase movement. Studies of the rate of chromosome movement (Barber, 1939; Ris, 1943) show no increase in velocity as the chromosomes approach the pole, as would be the case were a constant force acting across the space occupied by the spindle. If the force must be assumed to have any properties of an electric or magnetic field, the theory encounters the difficulty of the division figures with crowded or slanting metaphase plates in which chromosomes divide and the daughters move to opposite poles, regardless of the proximity of the pair to one pole. If a force is in-

volved, it must fluctuate, and moreover must be insulated from one pole and directed toward the other!

One can, in place of an attraction, conceive of the motivating force as a repulsion between sister kinteochores, but such a repulsion still does not supply the answer to the discrepancy between magnitude of force and rate of movement. It would in addition require a highly complicated resolution of forces in bent or multipolar mitoses, with the repulsion acting around corners. The possibility is rendered a little more credible by assuming that the spindle is a channeled structure allowing the chromosomes to move only parallel to its axis regardless of the direction of the repelling force. One must ask, however, what could be the nature of a force that could act selectively (autonomously) between each two daughter chromosomes without affecting the others.

Darlington (1936) proposes a channeling of forces along molecular causeways, the spindle fibers, and maintains that as a result of this channeling the chromosome, although repelled only by its sister and the centriole, would be exposed to negligible lateral repulsion. Thus the chromosome can move only toward the waning repulsion of the centriole, pushed by the greater force of the separating kinetochores. Consider, however, that chromosomes converge upon the centriole from the broad metaphase plate. This produces a configuration in which a body motivated by two repulsions acting at an angle less than 180° moves directly against one of the repulsions. This requires a heretofore impossible resolution of forces, and one is hard put to understand how any dielectric properties of water can explain the anomalous mechanics. Note that only the forces are channeled; there is no mechanical guidance of the chromosomes by structures comparable to the spindle tubes of Schrader.

Autonomous repulsion, that is, repulsion only between daughter chromatids, has as its main bugbear the motivation of the unpaired X chromosome in the heterotypic division. Bleier (1931), supporting the chromosome re-

pulsion theory with thought-provoking comparisons between heterosomes and hybrid univalents, proposes an auxiliary agency, the dividing spindle material, which sweeps up the lagging X and carries it to the pole. He overlooks the frequently occurring precession of the heterosome. Moreover, the V shape of a centrally attached X and the loss of acentric fragments require the same participation of the kinetochore as in the autosomes.

Dynamic theories must meet the additional general objection that the karyokinetic figure behaves as a structure, not as a field of force. It can be moved bodily, distorted, split longitudinally or transversely, and even dissected, meanwhile retaining the identity of its parts although the dynamic reltationships are completely deranged. Interruption of mitosis without subsequent disruption, by experimental agents or during the normal process of egg maturation, implies that the chromosomes while moving are in a state of equilibrium. This duality is improbable if only forces separate from structures move the anaphase chromosomes.

It is clear that the strong pull and slow movement during anaphase and the necessity of "beaming" forces in peculiarly selective systems are not compatible with movement emanating from surface tension or with a force acting between two separated bodies. The more complex hypotheses designed to accommodate these difficulties are built on equally untenable contradictions. With the force theories eliminated we are brought to the last group of motive agencies: expanding or contracting structures.

The theory of anaphase movement supplied by an expanding phragmoplast can be harmonized with chromosome autonomy and kinetochore activity if we assume that longitudinal segments of the spindle are activated individually, and push apart the kinetochores of each daughter pair. The theory has some morphological foundation inasmuch as the spindle in some forms can be seen to originate from a grouping of elements that arise singly in connection with each chromosome. Multi-

polar mitoses and unpaired chromosomes are as damaging to this theory as to its counterpart involving repelling forces. In a multipolar or bent spindle the expanding structure must somehow operate at an angle without buckling. An unpaired meiotic chromosome has no partner to supply a push. Dicentric chromosomes and even separating daughters of a normal chromosome, stretching straight along the spindle axis, leave no space for the hypothetical expanding body, and no points on the chromosome upon which it could obtain purchase. Centrifugation again supplies the final blow. A spindle separated into parallel halves by centrifuging holds both sets of chromosomes against a centrifugal pull, although no trace of a central spindle remains. No adaptation of the repulsion theories, be the agent force or structure, can explain this parallel pull.

The spindle fiber theory encounters no difficulty in those situations which invalidate the other theories. Each fiber, being an independent structure, can contract independently, whether the chromosome be paired or unpaired. A fiber can pull a chromosome to its pole regardless of the number of spindle poles and regardless of the position of the chromosomes in relation to each other. It can exert a pull when curved and when its half spindle is torn entirely away from the other half. Its rate of contraction as evidenced by chromosomal movement is that to be expected of a fiber (Rashevsky, 1941), and the strength of its hold upon the chromosome can be all out of proportion to that rate of movement. Yet the theory retains its original simplicity: a fiber which attaches to a side of the kinetochore and contracts when activated by the chromosome.

Some additional evidence favoring the traction fiber is worth mentioning. When by microdissection one end of a spindle is pulled out of the cell (Wada, 1935), the chromosomes follow, like a bunch of sausages on strings, and fixation after dissection shows the chromosomes connected to the pole by fibers curved in the direction the

needle was pulled. Many investigators have shown that physical and chemical agents (especially colchicine) destroy spindle fibers and spindle function simultaneously. Schmidt (1939) has reported that the fibers become less birefringent as anaphase progresses, as if the fiber molecules, rearranging to shorten the fiber, lose some of their longitudinal alignment.

Questions

What difficulties, then, remain in the way of the traction fiber theory? All the objections can not be removed until the mechanism of chromosome movement is completely understood, but answers to some questions can be set forth tentatively. Some facts considered inconsistent with the theory are not entirely so. A microneedle traversing a spindle does not appear to encounter fibers (Chambers, 1924), but in this case the injury inflicted by the needle may dissolve or weaken the fibers. The fact that chromosomes often override the poles of the spindle is brought against the idea of a structure merely pulling *to* the poles. Elongation of the phragmoplast may account for this, but it is not necessary to rely on this or on cytoplasmic currents for an explanation. Tardy chromosomes being pulled to the poles would be expected to push others ahead of them, even beyond the point of fiber attachment.

Those who object that the spindle fibers have no place to attach seem to consider it necessary for the fiber to attach somewhere outside the spindle, possibly in the cortiplasm. Anaphase movement of chromosomes in spindles displaced by centrifugal force shows that there can be no such external fastening. It is not necessary. The spindle itself is a rigid body braced against stress by its longitudinal structure. Fibers attached at the poles would require no additional anchorage.

The contractility of fibrils needs no defense. Contractility in both animate and inanimate protein fibers has been repeatedly demonstated. Are the same mecha-

nisms involved in contraction of the spindle fiber? As stated above, polarized light shows that molecular rearrangement is involved. A model for such a traction fiber can be seen in the peripheral threads of the unfertilized *Nereis* egg. This fiber, upon contact with the sperm head (chromatin!), contracts and pulls the spermatozoon to the egg surface.

In contesting the other theories of chromosome movement, it is not intended that phenomena upon which some are based are denied. It remains true that the spindle does expand during the division of some kinds of cells and that this expansion exerts considerable pull upon the chromosomes (Upcott, 1938), but we have seen that this can not be the essential mechanism of chromosome movement in most mitoses. Even where the chromosomes are moved by spindle expansion, the fiber apparently acts as an anchor for the chromosomes (Ris, 1943). Similarly, it is undoubtedly true that the chromosome carries an electric charge on its surface, and it seems reasonable that this has something to do with the disposition of the chromosomes, particularly during prophase and metaphase, but this is not the force producing the anaphase movement.

Indispensability of the traction fiber certainly has not been proved as yet. The varieties of mitosis and meiosis are so diverse that one should not be surprised if some were found to lack traction fibers altogether. At present we are safe only in maintaining that the spindle fiber exists and probably is a typical, if not universal, component of the mitotic figure.

NATURE OF THE FIBER

It must be admitted that we are not sure if we have actually seen the fiber which pulls the chromosome. Shaposhnikov (Chapochnikov, 1939) has described short anaphase fibers attached to the chromosome and structurally different from the continuous fibers, and many others have described and drawn fibers connecting chro-

mosome with spindle pole, but the cytological picture among the different organisms and with different methods varies too much for us to say that any one reveals the functioning organelle.

Experimental evidence indicates that from among the micellae or fibrils of the spindle, the chromosome selects or organizes a traction fiber which attaches to opposite sides of the kinetochore. Then, after division of the chromosome, it induces the fiber to contract. Attachment and contraction are separate processes. It was Bělař's idea (1929) that the traction fiber was formed from fluid that spread from the chromosome along the spindle fiber. This permits a chromosomal source of motivation of the fiber, allowing for autonomy. Shivago and Trukhacheva (Schivago and T., 1938) describe just such a liquid kinetic body which spreads along the fiber and then contracts. The traction cone seen in living cells by Fujii and Yasui (reported by Shimamura, 1940) may be of a similar nature.

Conclusions

There are one or more critical objections to the theories of anaphase movement of the chromosome, with the exception of the traction fiber theory. This theory alone is consistent with the numerous variations of normal mitosis and the evidence of experimental findings without amendments to its original simplicity. It requires merely that the kinetochore of the metaphase chromatid has the power to attach to the fiber approaching on its side of the chromosome and the power to cause that fiber to contract.

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DISTRIBUTION AND VARIATION IN POCKET GOPHERS, *THOMOMYS TALPOIDES*, IN THE STATE OF WASHINGTON II

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CRITERIA FOR THE CLASSIFICATION OF THE GOPHERS OF WASHINGTON

IN estimating the kinship of the various populations of gophers we have relied mostly on characters of color, skull and average size. Characters of skull and size were studied most carefully in the races about Puget Sound. The conclusions drawn from this study seem to apply as well to gophers from other places in Washington.

Color seems less freely responsive to factors of natural selection and microgeographic variation, at least to such as have operated in Washington in post-Wisconsin time, and as a consequence characters of skull and size present differences that better serve to separate populations. Color characters are less variable and often give clues to relationships not otherwise readily apparent. The following comments on color are based on a study of material from the entire state of Washington and not on material from the Puget Sound area alone.

The color pattern of *Thomomys talpoides* is agouti of a simplified type. Both dorsally and ventrally the fur is composed of a single kind of hair, with no differentiation into guard-hair and underfur. The agouti pattern consists of a long, sepia-colored proximal band and a short distal band of yellow to brown. Rarely a third band of pigment is present on the extreme tips of a few hairs in the fur, but it is so short that its effect on the total color is insignificant. This band probably is a vestigial feature and is not treated further in the present report. The amount of color exhibited by the two basic bands of the fur varies with the race.

Until extensive breeding experiments have been carried out with pocket gophers, a completely satisfactory analysis of the genetic factors involved in coat color can not be made. The genetic factors for color, which are discussed in the present report, are those of important systematic value. Storer and Gregory (1934) made a genetic interpretation of certain mutations in color in pocket gophers; they attempted, with considerable success, to relate the abnormal variations to known mutations in color of the rat, mouse, guinea pig and European rabbit.

In considering the problem of color we have found a mutant specimen of *aequalidens* (Mus. Vert. Zool. No. 86955), saved by S. H. Lyman, from Dayton, Columbia County, to be instructive. In it the proximal band is not normal sepia but is colored like, and continuous with, the yellow-brown of the distal band. In this animal the genetic factor for the color of the proximal band seems to be missing. The fact that the color of the distal band was continuous to the base of the fur led us to examine closely other races of pocket gophers. We found that in races in which the color of the distal band was pale, the proximal color was correspondingly pale. If the distal band was dark, the proximal band was dark. Two specimens of *yakimensis*, discussed in detail later, have alternating patches of light-colored and dark-colored fur. The proximal band of the distally light-colored fur is uniformly paler than the proximal band of the distally dark-colored fur. The evidence suggests that the factors for the color of the distal and proximal bands are independent of each other. The distal band seems to be only superficially a band, and to be that portion of the fur in which a pigment, uniformly distributed to the base of the hairs, is not obscured by a darker pigment that is present only proximally. The color of the fur proximally is produced by two pigments, one of which is continuous throughout each hair and one of which is restricted to the proximal part of the fur. When the uniformly distributed pigment is pale (the pallor or darkness can be

observed in the distal band), the fur is relatively pale proximally. When the uniformly distributed pigment is dark, the proximal band is darkened by the addition of the more deeply colored uniform pigment. If the proximal pigment be represented by A, and the uniform pigment by B, the actual color of the fur distally would be B, whereas the proximal fur would be A and B. If B is dark, A and B would be relatively darker than when B is pale.

The color of the proximal band of fur of *Thomomys talpoides* may be controlled by genetic factors for a pigment which does not vary in intensity, plus factors for a second pigment which does vary. The sum total of proximal color always varies with this second color which is seen in pure form in the distal band of the fur.

The postauricular patches on *Thomomys talpoides* result from the absence of the segment of the fur that normally bears the distal color. Actual measurement showed the fur of the postauricular patches to be shorter by several millimeters than the surrounding fur. In the mutant specimen of *aequalidens* there are no postauricular patches. The fur of the region usually occupied by the patch is as short as normal but is colored like the distal band. In normal animals the color of the postauricular patch, then, results from the pigment of the proximal band plus the pigment of the distal band. As is to be expected, the postauricular patch is darker in races with dark distal color than in races with pale distal color.

The problem of color in the distal band is more complicated but can probably be explained by assuming a series of multiple alleles. The color varies with each race, from dull yellow in *devexus* to rich chestnut in *aequalidens*. Racial intergrades within subspecific groups assume an intermediate color. In natural crosses between the *fuscus* group of gophers and the *douglasii* group, dominance is revealed. Where *aequalidens* intergrades with *fuscus*, near Pullman, Whitman County, the color is that of *aequalidens* but the cranial characters and

external measurements are those of *fuscus*. Intergrades between *aequalidens* and *wallowa* from the Blue Mountains likewise are colored like *aequalidens*, although the size of animal and size and shape of cranium are those of *wallowa*.

The race *yakimensis* seems to possess genes for the color of both *fuscus* and *devexus*, of the *douglasii* group; usually it resembles *fuscus*. Two topotypes of *yakimensis* (W. W. D. Nos. 1076, 1244) show alternate bands of *fuscus*-like color and *devexus*-like color on the back. The gray, *devexus*-like transverse bands are the fewest; they vary from 6 to 30 mm. in anteroposterior length and extend from one side of the animal over the back, to the other side. In every case, these bands *follow molt lines*. Seemingly the dominance of the *fuscus* color can be reversed to that of *devexus* if certain environmental conditions during the molt are suitable. Where *yakimensis* intergrades with *devexus*, the number of *fuscus*-colored individuals becomes progressively less as the range of *devexus* is approached.

The length of the distal color-band along the individual hair is, of course, regulated by relative length of the proximal color. The distal color is continuous to the base but is obscured basally by the proximal color. When the distal band of color of a gopher is short, allowing more of the dark proximal color to show through, the specimen appears darker. The length of the distal band of color is rather constant in each race but varies somewhat from subspecies to subspecies.

Storer and Gregory (*loc. cit.*) reported dutch spotting (partial albinism) in but five pocket gophers. We found no spotting in gophers of the *fuscus* group in Washington, but in every race of the *douglasii* group from the Cascade Mountains westward there is spotting.

In summary, then, study of color in pocket gophers of Washington shows the following important facts: Intergrades of races of the same subspecific group show intermediate color, but crosses between the two groups of sub-

species show dominance. There is evidence, in one case at least, that of *yakimensis,* that this dominance is produced by environmental conditions at a critical time. The proximal color of the fur was found to be influenced by the distal color, and therefore is of but little systematic value since its variation in intensity of color parallels that of the distal color. The same is true of the color of the postauricular patches. Color characters of systematic value include: color of the distal band of the fur, relative length of the distal color band, and relative size of the postauricular patches.

In our annotated catalog of races the color is briefly described. The color terms describe the distal band of the fur as it lies on top of the proximal fur, that is, the general color effect of the fur when brushed back. All capitalized color terms are those of Ridgway (Color Standards and Color Nomenclature, 1912). Where a single term applies to the color of two or more subspecies which actually exhibit small but constant differences in color, these differences are mentioned under the heading of *"Comparisons"* in the individual races involved. Where the relative length of the distal band of color plays an important part in the total color effect, that fact is mentioned.

Annotated Catalog of Races

The classification and naming of a group of animals as variable as the pocket gophers of Washington must necessarily be in some measure arbitrary. No rigid definition of a subspecies, based on amount or quality of difference, will suffice. For example, the population of gophers with the "internasal" bone is considered racially akin to the gophers of the same region which lack the bone. Under a rigid system of classification, a character like that provided by the accessory center of ossification might be of ordinal magnitude. In general, however, we have been guided by the following principles:

1. Because no two forms of pocket gophers occupy the same locality in Washington, and since intergradation

occurs where any two kinds come into contact, all pocket gophers in the state are considered as belonging to one species, namely, *Thomomys talpoides*.

2. The pocket gophers of Washington belong to two "subspecific groups" which had different post-Pleistocene histories and genetically are more different from each other than subspecies from within any one group of

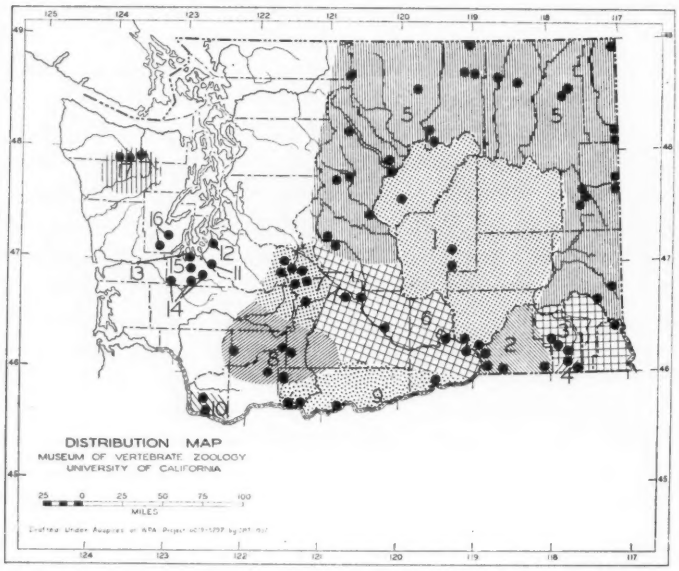

FIG. 5. Distribution of *Thomomys talpoides* in the state of Washington (spots indicate the sources of specimens). 1. *devexus*, 2. *columbianus*, 3. *wallowa*, 4. *aequalidens*, 5. *fuscus*, 6. *yakimensis*, 7. *shawi*, 8. *immunis*, 9. *limosus*, 10. *douglasii*, 11. *glacialis*, 12. *tacomensis*, 13. *pugetensis*, 14. *yelmensis*, 15. *tumuli*, 16. *couchi*, 17. *melanops*.

subspecies are different from each other. It should be emphasized that these groups of subspecies are groups of convenience only, and are not thought of as separate phyletic lines.

3. Our conclusions as to the systematic subdivision of the species *Thomomys talpoides* in Washington are summarized in the annotated catalog of races. In designating subspecies, we have considered not only the kind and

degree of difference, but the number of characters that differ. Although cranial characters exhibit greater in-

TABLE II

AVERAGE MEASUREMENTS OF ADUL MALE *THOMOMYS TALPOIDES* FROM WASHINGTON

Total length	Length of tail	Length of hind foot	Weight in grams	Condylobasal length	Length of rostrum	Zygomatic breadth	Interorbital breadth	Width of nasals	Width of rostrum
Two *devexus* from 10 mi. S Moses Lake, Grant County									
184	54	25	89	33.7	14.8	20.3	6.6	4.2	7.3
One *devexus* from 4 mi. W Pasco, Franklin County									
224	70	27	105	36.3	17.5	22.6	6.5	4.8	7.8
Five *columbianus* from Touchet, Walla Walla County									
213	60	29	...	37.2	17.2	22.2	7.1	4.5	7.7
Three *columbianus* from 1 mi. E Junction of Snake and Columbia Rivers, Walla Walla County									
211	72	27	122	37.4	17.5	22.6	6.7	4.3	8.2
Four *aequalidens* from 5–6 mi. SE Dayton, Columbia County									
202	57	26	...	37.4	16.7	23.2	6.9	4.6	7.8
Four *walloiwa* from Mountain Top and Stay-a-while Springs, Columbia County									
191	56	26	82	35.6	15.3	20.4	6.7	4.0	6.8
Three *fuscus* from Newport, Pend Oreille County									
189	54	27	...	34.4	16.2	20.3	6.3	4.4	6.7
Four *fuscus* from Conconully, Okanogan County									
191	50	26	...	34.2	16.0	19.6	6.3	4.3	6.8
Four *yakimensis* from Selah, Yakima County									
209	60	27	...	34.3	15.8	21.3	6.2	4.2	6.9
Two *shawi* from Mount Rainier, Pierce County									
227	72	32	...	38.1	17.3	22.2	6.9	4.5	7.3
Two *immunis* from Morrison Springs Ranger Station, Skamania County									
211	64	28	102	36.2	17.2	22.0	6.8	4.6	7.8
One *limosus* from White Salmon, Klickitat County									
210	55	30	...	36.2	16.6	21.2	6.5	4.5	7.4
Two *douglasii* from 5 mi. E Vancouver, Clark County									
227	68	30	148	38.3	18.1	23.7	7.7	5.4	8.5
Twenty *glacialis* from 2 mi. S Roy, Pierce County									
225	72	31	128	37.9	17.7	23.0	6.6	4.3	8.1
Thirteen *tacomensis* from 5 mi. SW Tacoma, Pierce County									
224	71	31	127	37.5	17.0	21.9	6.5	4.5	8.1
Fourteen *pugetensis* from 4 mi. S Olympia, Thurston County									
223	62	30	123	37.0	17.9	22.4	6.6	4.2	7.8
Eleven *tumuli* from 7 mi. N Tenino, Thurston County									
225	30	31	140	37.7	17.1	22.0	6.4	4.5	7.9
Twelve *yelmensis* from 1 mi. W Vail, Thurston County									
216	62	30	126	36.2	17.6	21.3	6.8	4.2	8.0
Twenty-one *yelmensis* from 1 mi. S Tenino, Thurston County									
213	64	29	121	36.8	17.6	21.7	6.5	4.3	7.7
Sixteen *yelmensis* from 2 mi. N Rochester, Thurston County									
215	63	30	117	36.3	17.6	21.1	6.9	4.1	7.3
Thirteen *couchi* from 4 mi. N Shelton, Mason County									
196	55	27	87	34.5	16.4	20.3	6.2	4.0	7.3
One *melanops* from Happy Lake Ridge, Callam County									
211	67	28	...	36.6	16.9	21.5	6.2	4.0	7.8

dividual and microgeographic variation than do color characters, the number of cranial characters is so large

TABLE III

AVERAGE MEASUREMENTS OF ADULT FEMALE *THOMOMYS TALPOIDES* FROM WASHINGTON

Total length	Length of tail	Length of hind foot	Weight in grams	Condylobasal length	Length of rostrum	Zygomatic breadth	Interorbital breadth	Width of nasals	Width of rostrum
Four *devexus* from 10 mi. S Moses Lake, Grant County									
184	55	25	71	31.6	14.3	18.7	6.4	4.7	6.6
Six *devexus* from 4 mi. W Pasco, Franklin County									
198	64	26	89	33.5	15.6	19.9	6.6	4.5	7.0
Three *columbianus* from Touchet, 450 ft., Walla Walla County									
109	58	28	...	35.8	16.0	21.8	6.9	4.6	7.4
Three *columbianus* from Wallula, Walla Walla County (approaching *devexus*)									
197	62	27	97	33.4	14.7	19.5	6.6	4.1	7.0
Four *columbianus* from 1 mi. E Junction Snake and Columbia Rivers, Walla Walla County									
203	61	28	96	34.8	16.1	21.2	6.7	4.2	7.0
One *aequalidens* from 5 mi. S Dayton, Columbia County									
201	59	27	...	36.7	16.2	22.0	7.0	4.6	7.8
Four *wallowa* from Mountain Top and Hompeg Falls, Columbia County									
180	52	25	...	31.8	14.6	20.1	6.5	4.2	6.7
Two *fuscus* from Newport and 8 mi. S Newport, Pend Oreille County									
186	57	26	76	34.5	16.6	19.8	6.8	4.0	6.9
Six female *fuscus* from Conconully, Okanogan County									
186	53	26	...	33.1	15.1	18.6	6.2	4.0	6.5
Three *yakimensis* from Selah, Yakima County									
191	56	25	...	32.1	15.7	19.7	6.2	4.2	6.7
Seven *shawi* from vicinity of Mount Rainier, Pierce County									
213	64	30	...	36.1	16.9	21.3	6.7	4.2	7.6
Eight *immunis* from 5 mi. S Troutlake, Klickitat County									
214	61	28	105	36.0	17.3	21.3	7.0	4.3	7.7
Two *immunis* from Morrison Springs Ranger Station, Skamania County									
212	58	29	101	35.6	17.2	20.9	6.6	4.4	7.6
Thirteen *limosus* from White Salmon, Klickitat County									
198	56	28	86	34.6	15.9	21.1	7.0	4.3	7.4
Ten *douglasii* from 5 mi. E Vancouver, Clark County									
213	63	30	117	36.5	17.2	21.7	7.3	4.5	8.0
Seventeen *glacialis* from 2 mi. S Roy, Pierce County									
220	71	30	116	37.1	17.5	22.2	6.4	4.0	8.0
Fifteen *tacomensis* from 5 mi. SW Tacoma, Pierce County									
196	57	29	104	35.7	16.4	20.8	6.5	4.1	7.7
Nineteen *pugetensis* from 4 mi. S Olympia, Thurston County									
205	59	29	96	35.6	16.2	21.1	6.4	4.0	7.4
Fourteen *tumuli* from 7 mi. N Tenino, Thurston County									
216	64	30	118	36.7	16.5	21.4	6.5	4.6	7.6
Ten *yelmensis* from 1 mi. W Vail, Thurston County									
211	63	30	107	35.7	16.6	20.8	6.6	4.4	7.8
Twenty-one *yelmensis* from 1 mi. S Tenino, Thurston County									
202	61	28	101	35.7	16.6	20.4	6.2	4.1	7.4
Thirteen *yelmensis* from 2 mi. N Rochester, Thurston County									
203	62	29	101	35.3	16.3	20.7	6.8	4.1	7.5
Nine *couchi* from 4 mi. N Shelton, Mason County									
191	53	27	79	33.8	15.6	19.7	6.0	3.9	7.1
Five *couchi* from Lost Lake Prairie, Thurston County									
189	56	26	81	33.7	15.5	19.5	6.0	3.8	7.4

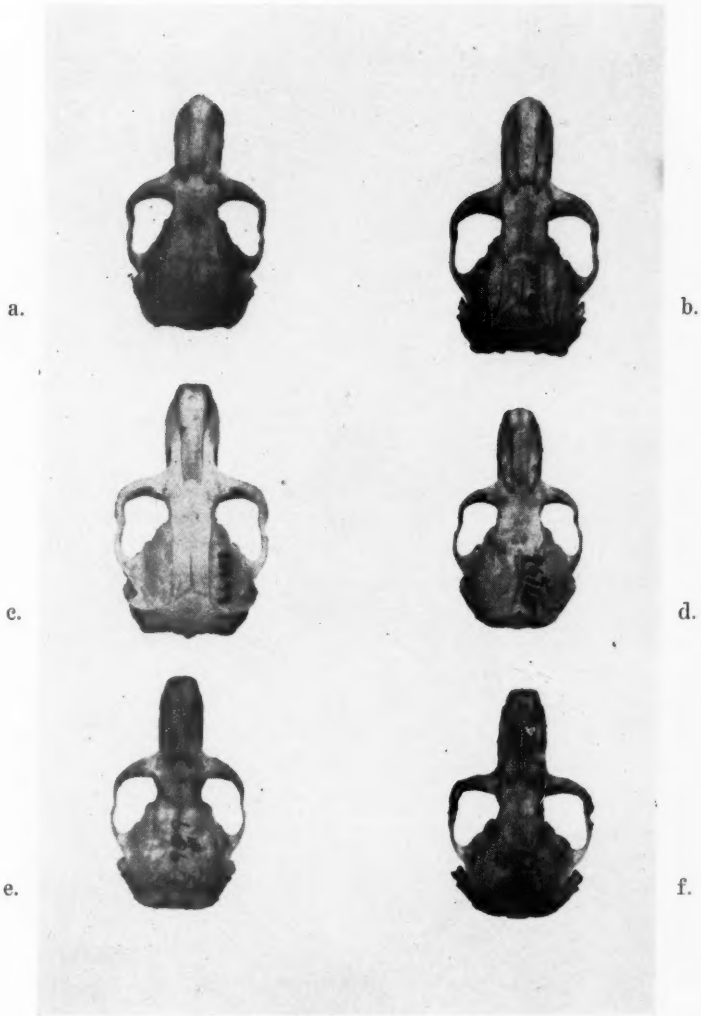

FIG. 6. Skulls of adult male *Thomomys talpoides* from Washington (natural size). a. *devexus*, 10 mi. S Moses L., Grant Co. (No. 835 VBS); b. *columbianus*, topotype (No. 44911 MVZ); c. *aequalidens*, topotype (No. 66403 MVZ); d. *wallowa*, Stay-a-while Springs, Columbia Co. (No. 87196 MVZ); e. *fuscus*, Pass Creek Pass, Pend Oreille Co. (No. 959 WWD); f. *yakimensis*, topotype (No. 1246 WWD).

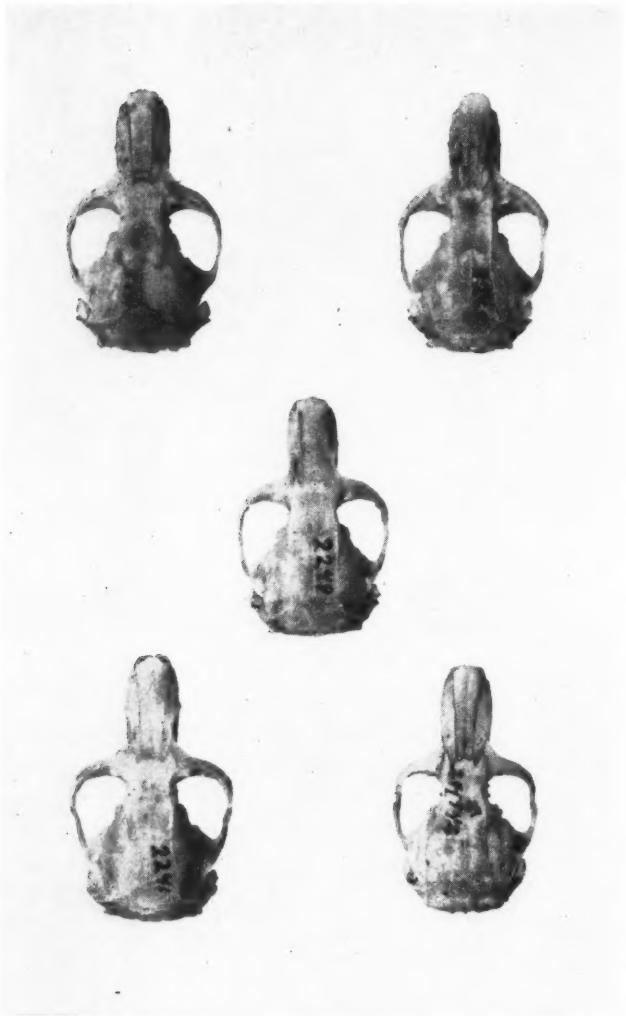

FIG. 7. Skulls of adult male *Thomomys talpoides* from Washington (natural size). a. *shawi*, Dewey Lake, Yakima Co., (No. 1923 WWD); b. *immunis*, topotype, (No. 2267 WWD); c. *limosus*, topotype, (No. 2249 WWD); d. *douglasii*, topotype, (No. 2241 WWD); e. *melanops*, topotype, (No. 241942 BSC).

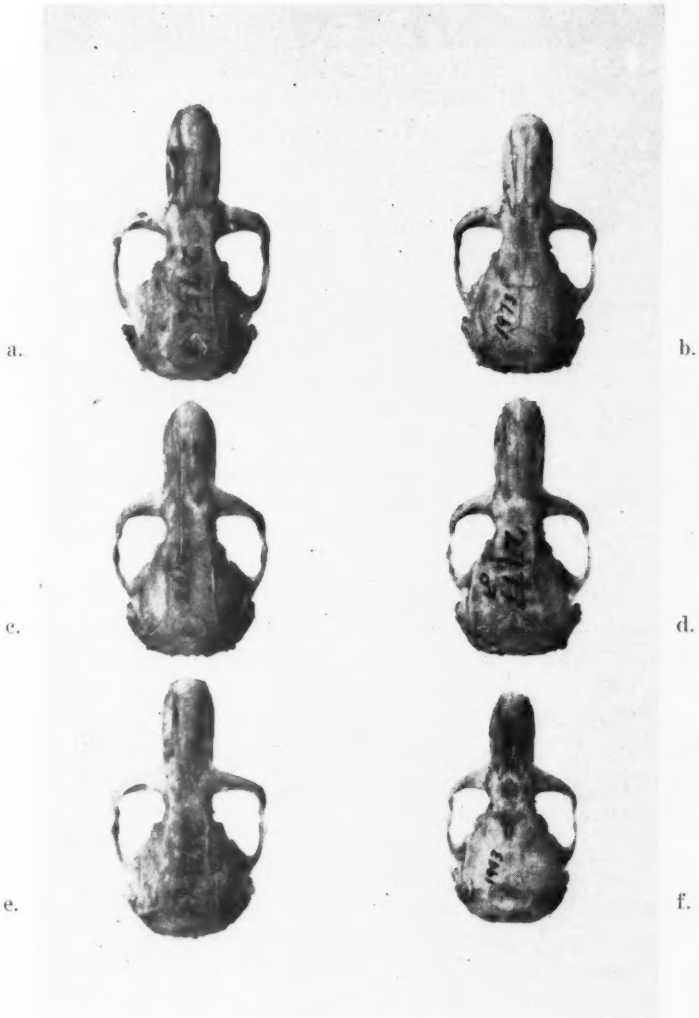

FIG. 8. Skulls of adult male *Thomomys talpoides* from Washington (natural size). a. *glacialis*, topotype, (No. 2756 WWD); b. *tacomensis*, 5 mi. SW Tacoma, Pierce Co., (No. 1973 WWD); c. *pugetensis*, topotype, (No. 2019 WWD); d. *tumuli*, topotype, (No. 2777 WWD); e. *yelmensis*, topotype, (No. 2131 WWD); f. *couchi*, Lost Lake Prairie, Mason Co., (No. 1993 BSC).

that measurements of the skull furnish the best criteria for the separation of gophers. Cranial features of all races occurring in Washington are shown in Figures 6, 7 and 8. Cranial measurements of systematic value are given in Tables II and III. Of all characters, those of body size seem to be most subject to individual and microgeographic variation, and most responsive to rapid selection and most prone to rapid evolution. Size, expressed by external measurements and weights, is recorded in Tables II and III.

The order of arrangement of the following systematic accounts of subspecies is one that permits comparison most readily of any one subspecies with geographically adjacent races. The list begins with *Thomomys t. devexus* from the Columbian Plateau of central eastern Washington, and is followed by *columbianus,* the race with which it intergrades on the south. After *columbianus,* races are listed in order, east to the Idaho boundary, then north to the Canadian boundary, then west to the Cascade Mountains, and then south along the Cascades to Mount Rainier, the range of *shawi.* Following *shawi,* races to the south are discussed until *douglasii* is reached. After *douglasii,* races to the west of *shawi,* in the Puget Sound area and the Olympic Mountains, are discussed. The arrangement of specimens examined follows the above order, first by county and second by localities within each county.

Comparisons of color are given under each subspecies heading and comparisons are restricted to races with adjoining geographic ranges or similar color. Comparisons of skulls and measurements are presented most briefly in tabular and graphic form (Tables II and III, Figs. 6, 7 and 8).

Thomomys talpoides devexus Hall and Dalquest

Thomomys talpoides devexus Hall and Dalquest, *Murrelet,* Vol. 20, p. 3, April 30, 1939.

Thomomys talpoides ericaeus Goldman, *Jour. Mamm.,* Vol. 20, p. 243, May 14, 1939. Type from Badger Mountains, Douglas County, Washington.

Type. Adult male, skin and skull, No. 84517, Mus. Vert. Zool., obtained 1 mi. WSW Neppel (now Moses Lake), Grant County, Washington, by W. W. Dalquest, May 30, 1938; original No. 688.

Range. The Columbian plateau of central eastern Washington.

Intergradation. Intergradation between *devexus* and *yakimensis* takes place at the mouth of the Yakima River, near Richland, Benton County. Intergradation with *fuscus* probably occurs along the eastern border of the range of *devexus.* Specimens from along the Columbia River in Walla Walla County show approach to *devexus* in pale grayish color. Indeed, specimens from southern Franklin County, on the southeastern corner of the Columbian plateau, show some approach to *columbianus* in large size and heavy skulls, representing an extreme microgeographic race or indicating that some individuals of *columbianus* have crossed the Snake River and entered the range of *devexus.* The pale color of certain specimens from the Columbia River Valley in eastern Benton County indicates some infusion of *devexus* blood into the population on this side of the river.

Color. Adult topotypes in fresh summer pelage are near Cinnamon-Buff in color.

Comparisons. This small race is the palest of Washington gophers. It is distinctly paler and grayer than *columbianus* or any other race with adjoining geographic range.

Remarks. The gray color of *devexus* best serves to distinguish it from other races of gophers. Specimens from both north and south of the type locality are larger over all and have larger skulls than topotypes.

Specimens examined. Total number 26, as follows: *Douglas Co.*: Badger Mountains, 2 (WSM).* *Grant Co.*: 1 mi. WSW Moses Lake, 1 (type); The Potholes, 10 mi. S Moses Lake, 7 (WWD 4, BSC 3). *Franklin Co.*: 4 mi. W Pasco, 350 ft., 15 (MVZ); 2½ mi. E, 1½ mi. S Pasco, 400 ft., 1 (MVZ).

* Names of collections are designated as follows:

BSC—Biological Surveys Collection, National Museum, Washington, D. C.
CRC—Charles R. Conner Museum, Pullman, Wash.
MVZ—California Museum of Vertebrate Zoology, Berkeley.
WSM—Washington State Museum, Seattle.
WWD—Walter W. Dalquest Collection, Berkeley.

Thomomys talpoides columbianus Bailey

Thomomys fuscus columbianus Bailey, *Proc. Biol. Soc. Wash.*, Vol. 27, p. 117, July 10, 1914.

Thomomys columbianus Bailey, *N. Amer. Fauna* 39, p. 106, November 15, 1915.

Thomomys talpoides columbianus Goldman, *Jour. Mamm.*, Vol. 20, p. 234, May 14, 1939.

Type. Adult male, No. 23722, U. S. Nat. Mus., Biol. Surv. Coll., obtained by C. P. Streator at Touchet, Walla Walla County, Washington, September 10, 1890; original No. 234.

Range. Walla Walla County, Washington, from the Columbia River east to the boundary of Columbia County, and from the Snake River south to the Oregon boundary.

Intergradation. Intergradation with *devexus* occurs along the Columbia River in western Walla Walla County. Intergradation with *wallowa* probably takes place in extreme southeastern Walla Walla County. Intergradation with *aequalidens* occurs at Dixie, Walla Walla County.

Color. Adult topotypes in fresh summer pelage are near Ochraceous-Orange in color.

Comparisons. This is the brightest and warmest-colored of Washington gophers. It can scarcely be confused with the dark *aequalidens* to the east. It is somewhat like *yakimensis* in color, but is paler and less glossy, with shorter distal color bands on the fur. The skull is larger and heavier than that of *yakimensis* or *fuscus*, with more angular, flaring zygomatic arches. Comparison with *devexus* is made under the account of that race.

Remarks. Along the Columbia River *columbianus* is especially gray in color, thus showing an approach to *devexus*. To the east, as the range of *aequalidens* is approached, *columbianus* becomes considerably darker.

Specimens examined. Total number 34, as follows: *Walla Walla Co.*: Touchet, 450 ft., 11 (MVZ); 7 mi. S Dixie, 4300 ft., 5 (MVZ); Prescott, 2 (approaching *aequalidens*) (MVZ); 2 mi. E junction Snake and Columbia rivers, 350 ft., 1 (approaching *devexus*) (MVZ); 1 mi. E junction Snake and Columbia rivers, 12 (approaching *devexus*) (MVZ); Wallula, 3 (approaching *devexus*) (MVZ 1, BSC 1, WWD 1).

Thomomys talpoides aequalidens Dalquest

Thomomys talpoides aequalidens Dalquest, *Murrelet*, Vol. 23, p. 3, May 14, 1942.

Type. Adult male, No. 66403, Mus. Vert. Zool., obtained at Abel Place, 220 ft., 6 mi. SSE Dayton, Columbia County, Washington, by S. H. Lyman, April 6, 1934; original No. M–28.

Range. Southeastern Washington east of the range of *columbianus*, exclusive of the Blue Mountains (see Fig. 5).

Intergradation. Intergradation with *fuscus* is shown by specimens here referred to that race from Pullman and Wawawai. Intergradation with *wallowa* occurs throughout the Blue Mountains of Washington. Intergradation with *columbianus* takes place near Dixie.

Color. Adult topotypes in fresh summer pelage are near Cinnamon-Brown in color.

Comparisons. This is the darkest race in eastern Washington. Specimens intermediate between *aequalidens* and the *fuscus*-group of gophers (*wallowa* and *fuscus*), resemble *aequlidens* in color but may be separated by their smaller size and smaller, less angular skulls and less flaring zygomatic arches. The occipital condyles of *wallowa* extend much farther posteriorly to the mastoid region than they do in *aequalidens*.

Remarks. The existence of this dark-colored gopher in an area possessing generally pale-colored mammalian races indicates the weakness of natural selective factors for color; at least such as have operated in post-Wisconsin time.

Specimens examined. Total number 16, as follows: *Columbia Co.*: Dayton, 1600 ft., 4 (MVZ); 5 mi. SE Dayton, 2150 ft., 3 (MVZ); 6 mi. SSE Dayton, 2200 ft., 4 (MZV); Jim Creek, 3200 ft., 11 mi. SE Dayton, 4 (MVZ). *Asotin Co.*: Clarkston, 1 (CRC).

Thomomys talpoides wallowa Hall and Orr

Thomomys quadratus wallowa Hall and Orr, *Proc. Biol. Soc. Wash.*, Vol. 46, p. 41, March 24, 1933.

Thomomys talpoides wallowa Goldman, *Jour. Mamm.*, Vol. 20, p. 234, May 14, 1939.

Type. Adult male, skin and skull, No. 54701, Mus. Vert. Zool., obtained at Catherine Creek, 7 mi. E. Telocaset, 3500 ft., Union County, Oregon, by R. T. Orr, June 29, 1932; original No. 570.

Range. Blue Mountains of southeastern Washington.

Intergradation. All the specimens examined from Washington are, to a greater or lesser degree, intergrades between *wallowa* and *aequalidens,* although the specimens from the range assigned to *wallowa* in Washington (see Fig. 5) are referable to *wallowa.*

Color. Adult topotypes in fresh summer pelage are near Ochraceous-Tawny in color. Most of the specimens from Washington are colored like *aequalidens.*

Comparisons. At the type locality, *wallowa* is colored like *fuscus.* Other than in color, the chief differences separating Washington specimens of *wallowa* from *fuscus* are: smaller size, smaller and weaker skull and occipital condyles ending relatively farther posteriorly to the mastoid region.

Specimens examined. Total number 10, as follows: *Columbia Co.*: Mountain Top, 4500 ft., 5 (MVZ); Twin Buttes Ranger Station, 25 mi. SE Dayton, 1 (MVZ); Stay-a-while Spring, 3 (MVZ); Hompeg Falls, 1 (MVZ).

Thomomys talpoides fuscus Merriam

Thomomys clusius fuscus Merriam, *N. Amer. Fauna* 5, p. 69, 1891.

Thomomys myops Merriam, *Proc. Biol. Soc. Wash.,* Vol. 14, p. 112, July 19, 1901. Type from Conconully, Okanogan County, Washington.

Thomomys fuscus fuscus Bailey, *N. Amer. Fauna* 39, p. 126, November 15, 1915.

Thomomys talpoides fuscus Hall and Dalquest, *Murrelet,* Vol. 20, April 30, 1939.

Type. Adult female, No. 24267, U. S. Nat. Mus., Biol. Surv. Coll., obtained from the mountains at the head of Big Lost River, Custer County, Idaho, by B. H. Dutcher, September 23, 1890; original No. 1847.

Range. The eastern part of the state, from Pullman, Whitman County, north to the Canadian boundary, and in the northern part of the state west, north of the Columbia River, to the Cascade Mountains, and thence south, west of the Columbia River, to Wenatchee and Merritt, Chelan County.

Intergradation. Intergradation of *fuscus* with *devexus* probably takes place along the eastern edge of the range of the latter race, but is not shown in specimens at hand. Intergradation with *yakimensis* takes place in the Wenatchee Mountain area (Lake Cle Elum, Kittitas County; Merritt and Wenatchee, Chelan County). Intergradation with *aequalidens* is shown in specimens from Pullman and Wawawai, Whitman County.

Color. Adult topotypes in summer pelage are near Ochraceous-Tawny. Washington specimens average slightly duller than the series of topotypes available to us.

Comparisons. This race is smaller and slightly browner, less orange in color, than *yakimensis.* Comparisons with *fuscus* and *wallowa* are made in accounts of those races.

Remarks. The range tolerance of this race is wide; edaphic or ecologic features that might serve as barriers to other races do not restrict *fuscus.* This is thought to account, in part, for the wide geographic range of *fuscus* in Washington, and for the few microgeographic races.

The name *myops* Merriam, proves to be based on a microgeographic race which does not differ in color, and differs but slightly in cranial characters, from typical *fuscus.* In all topotypes of *myops* at hand, the premaxillae extend little or not at all past the posterior end of the nasals. This character is variable over the range of *fuscus* in Idaho and Washington.

Specimens examined. Total number 92, as follows: *Whitman Co.*: Wawawai, 1 (CRC); Pullman, 8 (CRC). *Spokane Co.*: Cheney, 1 (BSC); Liberty Lake, 2 (BSC); Marshall, 9 (BSC); Spokane Falls, 6 (BSC); Spokane Bridge, 3 (BSC). *Pend Oreille Co.*: 8 mi. S Newport, 1 (WWD); 2 mi. S Newport, 1 (WWD); Newport, 5 (WWD 3, MVZ 1, BSC 1); Round Top Mountain, 2 (CRC 1, WWD 1). *Ferry Co.*: Sherman Creek Pass, 1 (WWD); 2 mi. E Republic, 1 (WWD). *Stevens Co.*: 5 mi. W Pend Oreille Lake, 1 (WWD); 15 mi. E Colville, 3 (BSC). *Okanogan Co.*: 20 mi. E Tonasket, 3 (WWD); 15 mi. E Tonasket, 5 (WWD); Chesaw, 1 (WSM); 6 mi. SE Okanogan, 1 (WWD); Duley Lake, 1 (WWD); Conconully, 3280 ft., 11 (MVZ). *Chelan Co.*: S end Lake Chelan, 2 (WWD); 3 mi. W Chelan, 1 (WSM); Lakeside, 1 (WSM); Lucerne, 1 (CRC); Lake Wenatchee, 1 (CRC); Wenatchee, 3 (WWD 2, CRC 1); Merritt, 12 (WWD 10, MVZ 2).

Whatcom Co.: Barron, 1 (CRC). *Kittitas Co.*: 5 mi. NW Cle Elum, 3 (WWD).

Thomomys talpoides yakimensis Hall and Dalquest

Thomomys talpoides yakimensis Hall and Dalquest, *Murrelet*, Vol. 20, p. 4, April 30, 1939.

Thomomys talpoides badius Goldman, *Jour. Mamm.*, Vol. 20, p. 242, May 14, 1939. Type from Wenatchee, Chelan County, Washington.

Type. Adult female, skin and skull No. 84518, Mus. Vert. Zool., obtained at Selah, Yakima County, Washington, by Peggy Burgner, November 27, 1938; original No. 1077 of W. W. Dalquest.

Range. The Yakima Valley area, east to the Columbia River, north to the Wenatchee Mountains, west to the Cascade Mountains, and south probably to the Simcoe Range.

Intergradation. Intergradation between *yakimensis* and *devexus* takes place at the mouth of the Yakima River. Intergradation with *fuscus* occurs over a rather wide area, from Cle Elum, Kittitas County, north to Merritt and Wenatchee, as might be expected from the migrational history of the two races. Intergradation with *shawi* occurs in the western foothills of the Cascade Mountains. Intergradation with *limosus* may take place on the northern slope of the Simcoe Range; gophers are not certainly known to occur there.

Color. Adult topotypes in fresh summer pelage are near Ochraceous-Tawny in color, and are slightly brighter and more orange than *fuscus*.

Comparisons. Compared with *shawi*, *yakimensis* is smaller and is orange, rather than dark grayish-brown in color. Comparisons with *fuscus* are made in the account of that race.

Remarks. The racial stock of *yakimensis* appears to have been a mixture of gophers of the *douglasii* group (*T. t. devexus*) and the *fuscus* group (*T. t. fuscus*) which, isolated in the Yakima Valley, subsequently deviated from both ancestral types.

Specimens examined. Total number 43, as follows: *Yakima Co.*: Selah, 18 (WWD 11, WSM 5, MVZ 2); Cowiche, 3 (MVZ); Zillah, 1 (CRC). *Benton Co.*: 2 mi. NW Richland, 400 ft., 1 (MVZ); S side of Yakima River,

2 mi. SE Richland, 9 (MVZ); 3 mi. W, 1 mi. N Kennewick, 375 ft., 11 (MVZ).

Thomomys talpoides shawi Taylor

Thomomys douglasii shawi Taylor, *Proc. Biol. Soc. Wash.*, Vol. 34, p. 121, June 30, 1921.

Thomomys talpoides shawi Hall and Dalquest, *Murrelet*, Vol. 20, p. 4, April 30, 1939.

Type. Adult male, skin and skull, No. 232807, U. S. Nat. Mus. Biol. Surv. Coll., obtained at Owyhigh Lakes, Mount Rainier, Pierce County, Washington, by G. G. Cantwell, August 9, 1919; original No. 1464.

Range. The central Cascade Mountains, from Mount Rainier south certainly to Signal Peak.

Intergradation. Intergradation between *shawi* and *immunis* probably occurs somewhere north of Mount Adams, but is not shown in material at hand. Intergradation with *yakimensis* takes place in the eastern foothills of the Cascades in Yakima County. No intergradation with *glacialis* occurs at the present time.

Color. Adult topotypes in fresh summer pelage are near Tawny in color.

Comparisons. This race is slightly paler and less rich in color than *immunis*. Comparisons with *yakimensis* are made in the account of that form.

Remarks. The separation of *shawi* and *immunis* seems to have been brought about by ecologic barriers. The habitat occupied by *shawi* consists of damp alpine meadows at considerable elevation, while *immunus* is found usually in dry, grassy clearings in open pine woods. Unfortunately, the major parts of the supposed ranges of both lie in rugged, inaccessible country. The habitat preferences of *shawi* were studied only on Mount Rainier, the northern border of its range; those of *immunis* were studied only in the southern part of its range, near Mount Adams.

Specimens examined. Total number 27, as follows: *Yakima Co.*: Goose River at Bumping River, 1 (CRC); 3 mi. NE Goose Prairie, Bumping Lake, 1 (BSC); McAllister Meadows, 2000 ft., 2 (BSC); McAllister Meadows, 2900 ft., 1 (CRC); S fork, Tieton River, 1 (CRC); head of Hindoo Creek, Mt. Aix, 6500 ft., 1 (BSC); Twin Sisters Lakes, 5300 ft., 1 (BSC); 2 mi.

SW Conrad Meadows, 4200 ft., 2 (BSC); Signal Peak, 4000 ft., 5 (BSC); Yakima Indian Reservation, 1 (BSC). *Pierce Co.*: Glacier Basin, 5935 ft., Mount Rainier, 5 (BSC, 4, CRC, 1); Owyhigh Lakes, 5100 ft., Mount Rainier, 3 (BSC, 2, CRC, 1); Dewey Lake, 3 (WWD).

Thomomys talpoides immunis Hall and Dalquest

Thomomys talpoides immunis Hall and Dalquest, *Murrelet*, Vol. 20, April 30, 1939.

Type. Subadult male, skin and skull, No. 84519, Mus. Vert. Zool., obtained 5 mi. S Trout Lake, Klickitat County, Washington, by W. W. Dalquest, July 27, 1937; original No. 395.

Range. From Trout Lake north, at least to Mount Adams.

Intergradation. Intergradation between *immunis* and *limosus* probably occurs less than 10 miles north of the Columbia River in higher land away from the river-valley meadows, a place from which no specimens are available. None of the specimens examined show intergradation.

Color. Adult topotypes in fresh summer pelage are near Tawny in color.

Comparisons. This race is paler and grayer than either *shawi* or *limosus*. The skull of *immunis* is larger and relatively longer than that of *limosus*, with flaring zygomatic arches (see Fig. 7).

Remarks. The northern, western and eastern boundaries of the range of this race can not be ascertained at present because of the lack of specimens from some critical but inaccessible places. Probably the range extends west of Mount St. Helens and east to the Simcoe Range.

Specimens examined. Total number 27, as follows: *Yakima Co.*: Gotchen Creek Ranger Station, 1 (CRC). *Klickitat Co.*: 5 mi. S Trout Lake, 9 (WWD). *Skamania Co.*: 1 mi. S Morrison Springs Ranger Station, 7 (WWD); Twin Buttes, 4300 ft., 2½ mi. SW Steamboat Mountain, 2 (MVZ); Cayuse Meadows, 3½ mi. SW Steamboat Mountain, 3800 ft., 5 (MVZ); Mount St. Helens, 3 (BSC).

Thomomys talpoides limosus Merriam

Thomomys limosus Merriam, *Proc. Biol. Soc. Wash.*, Vol. 14, p. 116, July, 1901.

Thomomys talpoides limosus Goldman, *Jour. Mamm.*, Vol. 20, p. 235, May 14, 1939.

Type. Adult male, No. 89724 U. S. Nat. Mus., Biol. Surv. Coll., obtained at White Salmon, Klickitat County, Washington, by J. A. Loring, June 26, 1897; original No. 4382.

Range. The Columbia River Valley from Paterson, Benton County, east to White Salmon, Klickitat County. Probably found also on the southeastern part of the Simcoe Range.

Intergradation. Intergradation between *devexus* and *limosus* occurs as far west as Paterson, Benton County. Intergradation with *immunis* must take place less than 10 miles north of White Salmon, Klickitat County. No intergradation with *douglasii* is apparent.

Color. Adult topotypes in full summer pelage are near Tawny in color.

Comparisons. Compared with *shawi, limosus* is slightly paler. Compared with *immunis, limosus* is considerably darker. Compared with *douglasii, limosus* is less yellow.

Remarks. *T. t. limosus* seems to be the western counterpart of *aequalidens,* which it closely resembles. Increased aridity is thought to have caused the removal of the Simcoe Bridge (see account of immigrational history) in the Columbia River Valley, thus isolating *aequalidens* in southeastern Washington and *limosus* on the Simcoe Range, west of the Columbia River. This same aridity is thought to have created conditions in the lower Columbia Valley favorable to the spread of gophers, and to have allowed *limosus* to spread westward as far as the type locality.

Specimens examined. Total number 29, as follows: *Benton Co.*: Paterson, 250 ft., 1 (MVZ). *Klickitat Co.*: 1 mi. NE Maryhill, 5 (MVZ); 1 mi. W Lyle, 3 (WWD); White Salmon, 10 (MVZ); 5 mi. W White Salmon, 10 (WWD).

Thomomys talpoides douglasii Richardson

Geomys douglasii Richardson, Fauna Boreali—Americana, Vol. 1, p. 200, 1829.

Geomys fuliginosus Schinz, *Mamm.*, Vol. 2, p. 136, 1845.

Thomomys douglasii Allen, *Bull. Amer. Mus. Nat. Hist.*, Vol. 5, p. 66, August 28, 1893.

Thomomys douglasii douglasii Bailey, *N. Amer. Fauna* 39, p. 116, November 15, 1915.

Thomomys talpoides douglasii Goldman, *Jour. Mamm.*, Vol. 20, p. 235, May 14, 1939.

Type. Obtained near old Fort Vancouver, Clark County, Washington, by David Douglas, probably in 1825, and probably no longer in existence (see Bailey, 1915).

Range. The Pleistocene gravel terraces (locally known as plains) of the Columbia River near Vancouver, Clark County.

Intergradation. None.

Color. Adult topotypes in fresh summer pelgae are between Ochraceous-Tawny and Ochraceous-Orange in color.

Comparisons. T. t. douglasii differs from all other gophers in Washington in that the postauricular patches are wanting or small and in that the zygomatic arches are markedly expanded anteriorly.

Specimens examined. Total number 15, as follows: *Clark Co.*: 5 mi. E Vancouver, 13 (WWD); Brush Prairie, 1 (WWD); Orchards, 1 (WWD).

Thomomys talpoides glacialis Dalquest and Scheffer

Thomomys talpoides glacialis Dalquest and Scheffer, *Proc. Biol. Soc. Wash.*, Vol. 55, p. 97, August 13, 1942.

Type. Adult male, skin and skull, No. 272033, U. S. Nat. Mus., Biol. Surv. Coll., obtained 2 mi. S Roy, Pierce County, Washington, by W. W. Dalquest, December 19, 1941; original No. 2672.

Range. Known only from the prairies south of Roy, Pierce County, Washington.

Intergradation. None known.

Color. Specimens in fresh winter pelage are nearest to Cinnamon.

Comparisons. Compared with *tacomensis, glacialis* is paler and more yellowish. The underparts of *glacialis* are distinctly more ochraceous than those of *tumuli, pugetensis,* or *yelmensis.* The skull of *glacialis* is relatively shorter and wider with more flaring zygomatic arches than those of other races from the Puget Sound area.

Specimens examined. Total number 50, all from the type locality (BSC).

Thomomys talpoides tacomensis Taylor

Thomomys douglasii tacomensis Taylor, *Proc. Biol. Soc. Wash.*, Vol. 32, p. 169, 1919.

Thomomys talpoides tacomensis Goldman, *Jour. Mamm.*, Vol. 20, p. 235, September 30, 1919.

Type. Young adult female, No. 231196 U. S. Nat. Mus., Biol. Surv. Coll., obtained 6 mi. S Tacoma, Pierce County, Washington, by G. G. Cantwell, December 24, 1918; original No. 857.

Range. Seemingly restricted to certain prairies near Steilacoom and prairies and some agricultural lands near Tacoma; all in Pierce County.

Intergradation. None known.

Color. Adult topotypes in fresh winter pelage are nearest to Hazel in color, but are brighter.

Comparisons. The especially rich hazel color of *tacomensis* distinguishes it from all gophers found about Puget Sound, save *couchi*, from which *tacomensis* differs in much larger size and in cranial characters (see Fig. 8).

Remarks. As far as we could discover, there are no gophers on the extensive prairies of the Fort Lewis area, between the ranges of *tacomensis* and *glacialis*. Mima mounds occur on the prairies 2 miles south of Spanaway, showing the existence in the past of a geographically connecting population.

Specimens examined. Total number 41, as follows: *Pierce Co.*: Tacoma, 9 (BSC); University Place, Tacoma, 3 (BSC); ½ mi. E Tacoma Narrows, Tacoma, 5 (BSC); 1 mi. S Day Island Bridge, Tacoma, 3 (BSC); 5 mi. SW Tacoma, 21 (BSC 6, WWD 15).

Thomomys talpoides pugetensis Dalquest and Scheffer

Thomomys talpoides pugetensis Dalquest and Scheffer, *Proc. Biol. Soc. Wash.*, Vol. 55, p. 96, August 13, 1942.

Type. Adult male, skin and skull, No. 272032, U. S. Nat. Mus. Biol. Surv. Coll., obtained 4 mi. S Olympia, Thurston County, Washington, by W. W. Dalquest, December 31, 1941; original No. 2022.

Range. Known only from prairies south of Olympia, in Thurston County, Washington.

Intergradation. None known.

Color. Topotypes in fresh winter pelage are nearest to Snuff Brown.

Comparisons. Compared with *tumuli*, *pugetensis* is

yellower in color, less grayish, and has a shorter, relatively wider skull. Dark patches on the sides of the neck distinguish *pugetensis* from all other gophers in the Puget Sound area, save *tumuli*.

Specimens examined. Total number 54, all from the type locality (BSC 26, WWD 28).

Thomomys talpoides tumuli Dalquest and Scheffer

Thomomys talpoides tumuli Dalquest and Scheffer, *Proc. Biol. Soc. Wash.*, Vol. 55, p. 96, August 13, 1942.

Type. Adult male, skin and skull, No. 272034, U. S. Nat. Mus., Biol. Surv. Coll., obtained 7 mi. N Tenino, Thurston County, Washington, by W. W. Dalquest, January 2, 1942; original No. 2781.

Range. Known only from Rocky Prairie, 7 mi. N Tenino, Thurston County, Washington.

Intergradation. None known.

Color. Topotypes in fresh winter pelage are between Cinnamon and Sayal Brown in color.

Comparisons. Compared with *yelmensis*, *tumuli* is larger, darker, and possesses dark patches on the neck.

Specimens examined. Total number 36, all from the type locality (BSC 30, WWD 6).

Thomomys talpoides yelmensis Merriam

Thomomys douglasi yelmensis Merriam, *Proc. Biol. Soc. Wash.*, Vol. 13, p. 21, Jaunary 31, 1899.

Thomomys douglasii yelmensis Taylor, *Proc. Biol. Soc. Wash.*, Vol. 32, p. 169, September 30, 1919.

Thomomys talpoides yelmensis Goldman, *Jour. Mamm.*, Vol. 20, p. 243, May 14, 1939.

Type. Adult male, No. 31916, U. S. Nat. Mus., Biol. Surv. Coll., obtained at Tenino, Thurston County, Washington, by C. P. Streator, October 24, 1891; original No. 1385.

Range. Grand Mound Prairie, near Tenino; Vail Prairie, near Vail; Rochester Prairie, near Rochester; all in Thurston County, Washington.

The original type locality was given by Merriam, (*loc. cit.*) as "Tenino, Yelm Prairie." At the present time the prairie at Tenino is known as Grand Mound Prairie. A prairie now known as Yelm Prairie is situated 13 mi. NE Tenino, and, as far as could be ascertained, no gophers exist there.

Intergradation. None known.

Color. Adult topotypes in fresh winter pelage are between Tawny-Olive and Sayal Brown in color.

Comparisons. This race differs from *couchi* in larger size and yellower, duller color.

Specimens examined. Total number 147, as follows: *Thurston Co.*: 1 mi. S Tenino, 63 (BSC 17, WWD 34, MVZ 12); 2 mi. N. Rochester, 50 (BSC); 1 mi. W Vail, 34 (BSC, 30, WWD 4).

Thomomys talpoides couchi Goldman

Thomomys talpoides couchi Goldman, *Jour. Mamm.*, Vol. 20, p. 243, May 14, 1939; Hall and Dalquest, *Murrelet*, Vol. 20, p. 38, August 10, 1939.

Type. Adult male, skin and skull No. 243092, U. S. Nat. Mus., Biol. Surv. Coll., obtained at Scotts Prairie, 4 mi. N Shelton, Mason County, Washington, by L. K. Couch; X-catalog No. 22896.

Range. Isolated prairies at the southeastern base of the Olympic Mountains; recorded from Scotts Prairie and Lost Lake Prairie, Mason County.

Intergradation. None known.

Color. Adult topotypes in fresh winter pelage are nearest to Hazel in color, but are brighter.

Comparisons. The rich hazel color of *couchi* distinguishes it from all other subspecies of gophers found in the Puget Sound area, save *tacomensis*, from which it differs in much smaller size.

Specimens examined. Total number 55, as follows: *Mason Co.*: 4 mi. N Shelton, 48 (BSC, 18, WWD 27, MVZ 3); Lost Lake Prairie, 7 (WWD).

Thomomys talpoides melanops Merriam

Thomomys melanops Merriam, *Proc. Biol. Soc. Wash.*, Vol. 13, p. 21, January 12, 1899.

Thomomys douglasii melanops Bailey, *N. Amer. Fauna* 39, p. 119, November 15, 1915.

Thomomys talpoides melanops Goldman, *Jour. Mamm.*, Vol. 20, p. 235, May 14, 1939.

Type. Adult female No. 90630, U. S. Nat. Mus., Biol. Surv. Coll., obtained at timberline at head of Soleduck River, Clallam County, Washington, by V. Bailey, August 28, 1897; original No. 6219.

Range. Alpine meadows of the high Olympic Mountains.

Intergradation. None known.

Color. An adult in slightly worn summer pelage is nearest to Tawny-Olive in color, but is duller.

Comparisons. Compared with *couchi, melanops* is larger, duller, and much grayer. Compared with *yelmensis, melanops* is duller, grayer, and has more black on the sides of the face. Compared with *shawi, melanops* possesses larger postauricular patches and much more black on the sides of the head.

Specimens examined. Total number 8, as follows: *Clallam Co.*: Timberline at head of Soleduck River, 2 (BSC); Cat Creek, 4500 ft., 2 (BSC); Happy Lake Ridge, 1 (BSC); Canyon Creek Divide, at head of Bogachiel River, 3, not typical (CRC).

SUMMARY

The descent of the Vashon-Wisconsin continental glacier eliminated all pocket gophers north of the drift border in the state of Washington. At the maximum extent of the ice sheet, gophers were present in the southern Cascade Mountains, on the Columbian Plateau, and in southeastern Washington. The dark-colored gophers of southeastern Washington were connected to those of the southern Cascade Mountains by a humid "bridge" along the Simcoe Anticline. This bridge, which was occupied by dark-colored gophers, isolated the pale gophers of the Columbian Plateau. With the retreat of the glaciers the Simcoe Bridge became more arid and no longer served as a geographically continuous habitat to connect the two dark-colored populations. The pale gophers of the Columbian Plateau then extended their range south, along the valley of the Columbia River. Gophers from Idaho invaded the land north of the drift border, recently cleared of ice, and extended their range to the west and south until they nearly encircled the pale gophers on the Columbian Plateau. The dark gophers of the southern Cascades pushed their range westward, on glacial outwash trains, to the glacial prairies of the Puget Sound area, the Olympic Mountains, and to river-terrace prairies in southwestern Washington.

The fossorial habits of pocket gophers, their limited tolerance with regard to ecologic conditions, and their

ability to exist for long periods of time in a single locality, all combine to make gophers subject to isolation by barriers that ordinarily do not restrict the movements of other vertebrates. As one result, pocket gophers within areas circumscribed by the more rigid barriers exist as independent populations in areas suitable to their needs. Such isolated populations behave as small, independent units and, as a result of different selective factors and the chance fluctuations of genetic factors, develop into microgeographic races. As a whole, the barriers separating these microgeographic races are constantly breaking down and reforming. Thus, isolation and intermingling of populations are constantly going on. Characters developed in microgeographic races might eventually spread throughout a subspecies as a result of successive chance "conquests" of other small populations or as a result of natural selection.

Color was studied in the seventeen races of gophers from the entire state of Washington. Differences in the color of the various races were found to be due principally to variations in the amount or kind of pigment present throughout the entire length of each hair. The variations in the amount or kind of this pigment are thought to be due to chance combinations of alleles of a multiple factor series. The gross color is modified by the relative length of the sepia-colored proximal band of the fur.

As a result of our now clearer understanding of the immigrational history and microgeographic variation of the pocket gophers of Washington, and in the light of our tentative genetic analysis of the variations in size, color and skull, we conclude that seventeen subspecies, all belonging to the species *Thomomys talpoides,* occur in the state.

Eight isolated populations of pocket gophers in the Puget Sound area, belonging to five subspecies, came from a common stock in post-Pleistocene times and now occupy similar but isolated habitats. Large samples of these populations were collected and studied in an effort to correlate differences in their habitats. Quantitative dif-

ferences in size and cranial construction were found to be correlated with the depth of the soil in the habitat occupied. Depth of soil seems to act as a selective factor in the fixation or loss of genetic factors, already present or newly acquired, in a multiple factor series for size. No correlation between the color of the gophers of the Puget Sound area and any measurable feature of their environments was found. It is concluded that selective factors for color are less strong than those for size and quantitative cranial characters.

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FISHES THAT PLAY "LEAPFROG"

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FISHES are given to leaping for many reasons: in fear or panic, to escape their enemies, to ascend waterfalls, to capture food and sometimes in sheer exuberance of spirits—in plain English, in fun or play. But the allegation set out in the title is so very extraordinary that the reader has already ejaculated—"Preposterous!" Maybe, but let us consider the evidence.

ORDINARY LEAPFROGGING

When boys play ordinary leapfrog, one called the "back" stands firmly with back to the leaper, with hands on knees and head bowed. The leaper takes a short run to the "back," places his hands on the other's shoulders and with wide-forked legs lifts his body head up (vaults) over the "back." The evidence that fishes likewise vault over sticks, bits of grass, a turtle or another fish will now be presented.

THE SALTWATER GARS—FAMILY BELONIDAE

These sharp-nosed marine gars are nearly all leapers and many accidents to fishermen have resulted from this habit. But before we consider the earliest record of the leapfrog habit in the young of these fishes, a biographical note is in order with reference to the man who made this record and to the locality where it and other observations have been made.

C. F. Holder spent a good part of his most impressionable years (11–18) at the Dry Tortugas, Florida, those last farflung outliers of the great Florida Reef. Here his father, Dr. J. B. Holder, was surgeon and health officer to the Federal Military Prison on Garden Key from 1862 to 1869. The son's life during these years seems mostly to have been spent on the reefs and the channels in between. As an outcome of his many adventures at the

Tortugas, he has written a series of most interesting books dealing with the fishes of the Florida Reef.

In an early book (1892) he gives the first account so far found of this interesting leapfrog habit of fishes. It reads as follows:

"Keep still!" whispered Long John [the fishing mentor of the boys at Tortugas in the early days]. "Keep still, and you'll see a game of leap-frog."

And surely enough they did, but the "frogs" were a turtle and the fish. The hawksbill was floating with its back several inches out of water, when suddenly a garfish leaped completely over it. Another made the attempt, half-turning in the air, two more followed suit—one turning a somersault—while still another, not quite so dexterous, failed in his act of lofty tumbling, and landed plump on the turtle's broad back, startling it so that it dived out of sight.

"I didn't know that fishes played games before," remarked Harry.

"They do, though," replied Long John; "and, as for these fellows, they give that poor turtle no peace. The minute he comes to the surface they begin their tricks, and if they can't jump over him they find some floating stick or straw and practice on that!"

Holder's account is illustrated by the accompanying drawing (Fig. 1), the only portrayal of this habit known to me. If only there were photographs or a motion picture film of this interesting performance.

In a later book (1899) Holder again writes of these leapfrogging fishes at Tortugas as follows in a section entitled "The Games of Animals":

Fishes have a decided sense of humor, judging from certain exhibitions that have been observed; the young especially have numerous games or methods of amusement; and their mischievous natures can best be appreciated when a large school is under observation. Through the flooring of a wharf in tropical waters at Fort Jefferson, Tortugas, I have often watched the varied throngs unsuspected and unseen. Such games and sports as they indulge in! Now a floating straw is discovered on the surface, and over it with a daring leap the leader goes, followed by the rest, until the leapers in a continuous glistening stream dart into the air.

The game of leaping over various objects, I have noticed in many fishes, especially in the young garfish; and in an aquarium built out into the water at Garden Key I have frequently seen them leaping over a hawksbill turtle that floated on the surface. This game at the expense of the turtle was kept up for some time, until a garfish in leaping landed fairly on the sleeper's back, when the astonished and indignant turtle took a long breath and dashed away, scattering the assembled fishes far and wide.

Fifty years (1912–1915) after Holder, I realized a life-long ambition by going to Tortugas to study its fishes—at the Marine Biological Laboratory of the Carnegie Institution of Washington with that prince of directors, Alfred Goldsborough Mayor, in charge.

On the floor of that wharf (renewed many times since Holder's day) I laid down time after time and through the cracks watched the fishes. But never once, to my keen disappointment, did I see the leapfrog game. However,

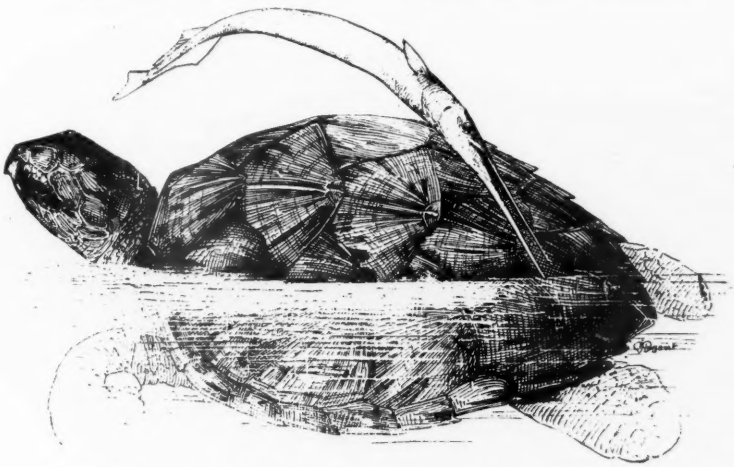

FIG. 1. A marine garfish (family Belonidae) leaping over a sleeping turtle at Fort Jefferson, Garden Key, Dry Tortugas.

this game had not been discontinued, and other men have later been more fortunate.

Strongylura (*Tylosurus*) is the genus of the Belonidae (needlefishes) to which all the identified leapers at Tortugas belong. Holder unfortunately did not give the scientific name of his fish, but, as Fig. 1 shows, it is surely a needlefish. It is now known that three species of Strongylura there practice leapfrogging—*ardeola*, *raphidoma* and *notatus*—named in the order of their addiction to this interesting practice. The ascertained facts of the leaping of these fishes will now be given.

Following some 60 years after Holder, W. H. Longley (with whom I worked in the laboratory on Loggerhead Key during the summers of 1913–1915) made the next observations of the leaping gars at Tortugas. Hildebrand, who after Longley's death in 1937 wrote the report on Tortugas fishes (1941) from Longley's incomplete MS. and fragmentary notes, thus quotes him on the behavior of *Strongylura raphidoma:*

At the dock I noticed *S. raphidoma* giving an exhibition of its interesting play. Five or six specimens were jumping over a piece of floating paper. Sometimes one would go back and forth quickly as many as three times. Sometimes one would put its snout slowly above the paper and then quickly glide across it; more usually they would make a clear leap. One caught its beak in the water after leaping and turned a somersault (apparently accidentally). This morning [July 9, 1923], the fish were jumping across a floating feather, and two larger fish were jumping across the floating body of a fish of their own species.

In 1929, C. M. Breder studied fishes at the Tortugas Laboratory and made more extensive observations than any one else has ever done on the leapfrog habit of the fishes of the family Belonidae. Of his studies he made a preliminary report later in the year.

When he described this interesting procedure, he did not know of Longley's observations, which were made earlier but were not published until four years after his untimely death in 1937. Thus Breder's careful studies, though made later, were published earlier (1929). Here is what he saw and recorded in two articles.

Observations were made on the habit of fishes of the genus *Strongylura* of vaulting over small floating twigs, straws, etc. *S. ardeola* seems most addicted to the practice, with *S. raphidoma* and *S. notatus* following in the order named. Sometimes a single fish would leap back and forth as many as a dozen times over a single straw. It is thought that the function of this well-marked habit is that of scratching to remove ectoparasites, for it was noted that usually some part of the fish was rubbed against the straw in passing. Second leaps were most often noted when this did not succeed. It is noted in this connection that *S. ardeola,* which was most given to the habit, also most frequently harbored ectoparasites, such as argulids, etc. These fishes, living almost entirely at the surface, do not have rocks for purposes of scratching, such as do bottom fishes, and it is inferred that they make use of what floating objects they may for such purposes; this apparently playful act seeming to have a very practical function.

In a fuller report (1932) of his Tortugas studies, Breder writes in more detail of this habit in fishes of the family Belonidae as follows:

With a shoal of such fishes of a dozen or more, the throwing of a small splint or straw in their midst will, in the writer's experience, invariably cause at least one to leap over it. Usually several will leap and sometimes a single individual will vault back and forth repeatedly. In carrying out such experiments, small sticks about $\frac{1}{8}$ inch square and from 4 to 12 inches long were offered to fishes from 12 to 16 inches long. A few statistical comments were made as follows:

Length of stick	*Length of fish*	*No. of fish leaping*	*No. of leaps*
4 inches	12 inches	2	1 each
12	14	1	1 (Tried 3 times before success)
8	12	4	1 each
8	12	1	9 times back and forth
6-inch piece of *Cymodocea*	12	1	3 times back and forth

This gives a fair idea of the reactions of a small school of these fishes to such floating objects before they drift out of the range of the school proper. An interested fish will seldom go very far from his school in following such a floating stick for purposes of leaping.

The actual action in leaping is most often as follows: First the fish will swim up slowly to the stick so as to be nearly at right angles to it (in a horizontal plane) and gently protrude the beak through the surface of the water, sliding the tip over the stick. Usually if the stick is too small and gives way too easily, or too large and gives way too little, the fish will withdraw. If it is of the proper buoyancy and sinks ever so little under the weight of the beak, a violent tail action follows and the fish clears the water, but in such a manner that usually part of the body rubs against the stick in passing and the fish falls to the other side, from which it may turn and leap back again.

Tylosurus raphidoma uses much more physical effort to accomplish this performance and is less inclined to show interest in such floating objects.

Then he repeats his argument, set out in Year Book No. 28 and quoted above (1929), that this action is for the purpose of ridding the fish of external parasites, and concludes thus: "This species, *T. raphidoma,* was commonly parasitized by some hirundid (?). A few were commonly seen on young *raphidoma.* In all cases, however, they dropped off on capture"—from which one gets an idea as to the ease with which they can be scraped off when the leaper rubs against the stick.

As the quotations all show, Breder has gone at the study of this behavior in thoroughly scientific fashion,

and made it clear that in his leapers the action is purposive—the scraping off of parasites.

The Herring, Clupea harengus, also Plays Leapfrog

In 1931, Breder (1932) was fortunate in seeing this fish also play leapfrog off Block Island, northeast of Montauk Point, Long Island. Here is his account of its action.

> On July 10, 1931, specimens about three inches long in large schools were observed to leap over broken fragments of *Zostera* in a manner similar to that described for various Belonidae at the Dry Tortugas. . . . The action was clearly similar, although more frequently specimens were noted to scratch themselves on entirely submerged fragments. This behavior on the part of three clupeids seems to be quite intermediate between the specialized scratching activities of belonids and the more generalized performances of various bottom fishes.

Leaping by a Sardine

Earlier in this article, Holder is quoted that he has noticed this behavior in "many fishes," but he does not name them. In a later and general article (1913) on leaping by fishes, he repeats the statement about the gars leaping over the turtle and then adds "I also observed [at Tortugas?] small sardines leap over a floating twig." But he gives neither details nor the scientific name of the fish, and the name sardine in colloquial usage may mean any small fish.

Atherina harringtonensis, a Leaper at Bermuda

William Beebe thus describes (1932) the behavior of these little fish at Bermuda:

> With a quiet school of Silversides and a wooden match . . ., I can magic play out of the usually serious, preoccupied little fish. A sinking pebble bores through a school of these . . . but a small splinter of wood or match thrown on the surface above the school has almost no effect. A few, directly beneath, may flinch slightly, but after a minute one, two, several, will drift up to the bit of wood and begin to leap over it. First one, then another goes over the hurdle, from this side or that, sometimes balking at the start and swimming away, more often flinching sideways, a leap clear of the surface, but very unlike the high, forward course when fleeing for life from an impi [army] of mackerel. This may accomplish some real purpose, either practice or achievement, to which we have no clue, but as far as appearances go, it is sheer exuberance.

John Tee-Van states (in a personal communication) that, while working at Bermuda with William Beebe in 1929–1931, he has at various places and times seen Atherinas (generally only one or two) play the leapfrog game. They vaulted over matchsticks or bits of straw on days when the water was calm, and in each case the leaping was continued for awhile as if the fish were enjoying itself. Their vaulting did not differ from the performance recorded by Beebe.

Apparently this playing leapfrog by small fishes at Bermuda is no new thing. Mr. Hawthorne Daniel, formerly editor of *Natural History* in the American Museum, told me some years ago that in November, 1927, he saw a little fish so performing in the channel off the Aquarium at Flatts. From a school of small fishes in the channel, one detached itself and, finding a floating twig a little distance away, played its game all by itself. It would swim up to the twig and push it with his nose. Then it would back off a short distance, and take a run to and leap over the twig. Then instead of leaping back, it would swim under the twig to the starting point, and repeat the performance. This was done a number of times. Mr. Daniel did not know what the fish was. Probably it also was *Atherina harringtonensis*.

Atherina araea of Haiti a Leapfrogger

John Tee-Van states that, in 1927, while studying fishes in Port-au-Prince Bay, he observed Atherinas of this species leaping over sticks and straws. Generally the leaping was done by a single fish or at most by two, and on quiet days. "There was very little control by the fish of its movements when it was in the air. It either leaped over the stick and dived into the water head first, or landed on its side, but apparently without injury since the distance was small. This performance was repeated, as if the little fish found it enjoyable."

This leaping by these Atherinas singly is interesting, since these small fishes are usually found in schools.

And now to be recorded are unpublished first-hand accounts of observations on the leaping habit made in the vicinity of New York by two men in the American Museum. Both are anglers and as such have frequently observed leapfrogging fishes. These observations they have kindly reported for inclusion in this article.

THE SILVERSIDE, MENIDIA NOTATA, ALSO A LEAPFROGGER

Louis Monaco has seen this behavior in these little fish in Sheepshead Bay on the southeastern ocean side of Long Island. Usually during September the waters are alive with these small fish, locally called "fish bait" or "spearing"; and here is what they do:

> Year after year, while fishing for snappers and using a cork bob, I have watched with amusement and fascination the antics of these little fish. The fishing line attached to the top of the cork or bob forms a little loop which rises above the surface of the water when the line is slowly drawn in, or sinks slightly under the surface when the line is let out. As long as the water is quiet and not disturbed by passing boats, these fish seem to have a lot of fun leaping over this loop. They leap out of the water and over the line whether the line is slightly under the surface or on the surface and will make a high-jump over it if the line is above the surface. The fascinating part of their leaps over the line, when it is above the surface, is whether or not they will make it. Most of the time they hit the line and bounce back, not having cleared it. Their leaps are not graceful and they often turn over in the air, land sideways, or tail first instead of head first. I have seen them do the same thing over a matchstick thrown in the water. In either case so many follow in succession at times that it seems to be a game of "follow the leader."

John Germann has seen like behavior of these same "spearing" and here is his description of it:

> While sailing on Long Island Sound, I have often been entertained by the sight of "spearing" leaping back and forth over floating stalks of grass, and over bits of driftwood from the size of a lath to that of a broom handle. The number of leapers varies from one or two to a small school of possibly six or eight. They leap over, turn around and leap back, seemingly in play, or in the indulgence of an acrobatic sport. This habit is so well established, that (especially with guests aboard) I always steer for any small floating objects, since the fishes are sure to leap and the sight never fails to please.

This concludes all the accounts (published and verbal) that I have come upon of ordinary leapfrogging by fishes.

But there are now to be recorded instances of a much more unusual type of such action. These are brought together in a section bearing the title:

FISHES THAT PLAY SOMERSAULT LEAPFROG

This is another form—a variant—of the leapfrog game with boys. The "back" is always a stout fellow chosen to withstand shock and weight. The "back" plants himself solidly with hands on knees and head bowed. The runner takes a short start, and when he approaches the "back" places his hands on the latter's hips, throws his feet up in the air, rests his head on the "back's" shoulders, turns a somersault heels-over-head, alights on his feet and after a short run recovers himself. This calls not only for more strength and agility but also for more judgment and coordination than does the ordinary leapfrog game. That fishes also do the somersault or tail-over-head leapfrog act is as new to the present writer (who for years has been collecting accounts of the ordinary kind) as it is to the readers of this article.

Holder in his first acount of the fish vaulting over the turtle says that one turned a somersault, but does not explain. However, Longley does, for he says that "One *Strongylura raphidoma* caught its beak in the water after leaping and turned a somersault (apparently accidentally)."

Fortunately, there came, at this point in these studies, a letter from Mr. Louis S. Mowbray, director of the Bermuda Aquarium, describing how three kinds of fishes in the waters around those islands continually and normally do the somersaulting leapfrog act. The information he gives is based on personal observations extending over a period of years on performances of "at least several hundred times." This action of these three fishes was always noted "when the water was quite smooth though not necessarily in a flat calm." The first of these fishes are those which also play the simple game of leapfrog as described above. This is a very interesting point.

THE SOMERSAULTING ATHERINA HARRINGTONENSIS AT BERMUDA

Of these Mowbray writes as follows:

The sight of this Atherina "flipping" is very common around harbors. The fish shows a preference for wooden match sticks, while in other places it will be a thin twig or single blade of grass.

The action is thus performed. The little fish approaches slowly and pushes the chin of the lower jaw against the object and with a quick flip of the tail, aided no doubt by the pectorals and ventrals, it leaves the water tail first and completes a somersault tail-over-head over the floating object landing almost invariably on its side and facing at a right angle to its former direction. The greatest number of consecutive flips that I have ever observed of a single Atherina was 9. This was done over a matchstick in Harrington Sound, and was observed at a distance of about 25 feet. But as the maximum length of Atherina is slightly under 3 inches, it was impossible to determine whether this act was done to remove a common louse-like parasite or for play. I really believe that it was a combination of both.

"FLIPPING" OF TWO HEMIRAMPHID OR HALF-BEAK FISHES

These fishes are close relatives of the Belonidae, and being leapers it is not surprising that they also play leap-frog. But it is rather surprising that they play the somersaulting instead of the vaulting game of their cousins, the Belonids, at Tortugas.

Hemiramphus brasiliensis, the balao, has been seen in the "flipping" act many times by Mr. Mowbray. Here is what the fish does:

The balao will approach and inspect some small floating object, such as a match box, or a thin flat piece off a wooden box, or a large single "leaf" of a seaweed which has floated to the surface. Then he will put the tip of his long lower jaw under the object and at the same time give a flip which almost invariably lands him tail first on the other side of the object and on his side generally but facing the opposite direction. This may be repeated five or six times within twenty seconds. Once I saw three fish of this species performing at one time on a single piece of box wood about 15 inches long. This was in Harrington Sound, behind the Bermuda Aquarium. It was the only time that I had seen more than one fish flipping at one time, so I recorded it then and there.

Hyporhamphus unifasciatus, another half-beak, performs similarly, but since it is not so common as the other two fishes in my fishing areas, I have made no special observations on it, though the performance shows no apparent difference from that of the other fishes. I have never seen one of these fish land head first—except when it was very obviously an accident due to a poor

flip. *H. unifasciatus* is a small fish only about five inches long while the balaos average 10 to 12 inches in length.

Given herein are accounts by 7 observers of ordinary leapfrogging by 7 species of identified and 2 of unidentified fishes in such widely separated regions as Block Island, Long Island (both shores), Bermuda (various localities), Tortugas and Port-au-Prince Bay, Haiti. In addition there are accounts by one scientific man ("based on hundreds of observations") of somersault leapfrogging by 3 species of fishes in Bermuda. These multiplied observations in these widely separated localities lead inevitably to the conclusion that this curious action is by no means of infrequent occurrence. However, these are all the accounts, published and verbal of this curious behavior in fishes that have come to light in the course of this study. Probably other such observations are buried in books and systematic articles or indeed have been made but never published. It is hoped that the gathering and publishing of the above accounts may lead others to watch for and bring to light their observations of this curious behavior in these and other fishes.

HOW AND WHY HAS THIS LEAPFROG HABIT ARISEN?

Two answers have been suggested. But, as noted, Breder is the first to suggest an answer based on careful scientific studies. From close observation of the leaping garfishes at Tortugas, he found the most common leaper, *Strongylura ardeola,* to be infested with ectoparasites, and that in leaping most generally some part of its body scraped the stick. His observations surely establish the fact that his little gars were trying to free themselves from external parasites. But his report of the leaping of small clupeids off Block Island is by no means so conclusive. One other man only has suggested the freeing of the fish from parasites. Mowbray notes that *Atherina harringtonensis,* a leaper at Bermuda, harbors ectoparasites. But he was not able to say whether the leaping was

to scrape off such or in play. Indeed he thought that it possibly partook of both purposes. Then the question comes—"Do all leapfroggers leap to get rid of parasites?"

C. F. Holder, at Tortugas sixty or more years before Breder, was convinced that the fishes were doing this in play. Certainly there was no scraping when the gars leaped over the sleeping turtle—for at the first touch it awoke and dived. Moreover, Holder's little gars followed their leader over the straw "in a continuous glistening stream."

In Holder's latest article (1913), bearing the title "How and Why Fishes Leap?," I have looked in vain for evidence of rubbing off of parasites. However, this is a general article on leaping by various fishes for various reasons. Of the leapfroggers, he reiterates that, so far as he could discover, their leaping was, like that of children over an obstacle, done in fun.

Furthermore Longley's gars leaped over a piece of floating paper, a feather, and "two larger fish were jumping across the floating body of a fish of their own species." Apparently these fish did not touch the objects over which they leaped, and no "scratching" was observed.

At Bermuda, Beebe concluded that the little Atherinas were leaping in "sheer exuberance." Tee-Van states that both at Bermuda and Haiti the Atherinas "leaped as if they found it enjoyable." And at Bermuda, Daniel's little fish certainly played a game, while Mowbray has seen an Atherina leap as many as 9 times consecutively, and a Balao leap 5 or 6 times in 20 seconds. Furthermore, he has seen three of these fish leap at one time over a 15-inch strip of wood.

Monaco's observations of silversides in Great South Bay near New York City indicate plainly that, with these little fish, the leaping over the fisherman's line in close succession is purely a matter of sport—no "scratching" was observed. This is confirmed by Germann's account.

Among Breder's young gars, a "single individual

would vault back and forth repeatedly''—in one case as many as nine times. To me this savors of play as well as of possible utility.

It is well known that the young (and even adults) of the higher animals (mammals especially) are given to play. One need not labor the point, but all know of the play of wild mammals; otters young and old play on their toboggan slides, and fawns and young foxes chase each other in fun. Birds likewise have their games. In short the play instinct seems fundamental—certainly in the higher animals.

To me it appears that what seems to be primarily a sport in these leapfrogging fishes has in certain ones assumed a utilitarian function. At any rate both things seem to be factors in this very curious habit. More and more widely diversified observations are needed, and snapshot photographs are special desiderata.

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REVIEWS AND COMMENTS

EDITED BY DR. CARL L. HUBBS

In these section reviews and notices of current publications on general biology emphasis is given to books and major articles which fall within the special scope of The American Naturalist, in that they deal with the factors of organic evolution. Reviews and Comments are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

The Woods Hole Marine Biological Laboratory. By Frank R. Lillie. Chicago: University of Chicago Press, 1944: i–ix, 1–284, 28 figs. $4.00.

Aided by E. G. Conklin, with whom joint authorship was originally planned, Frank Lillie presents a detailed and well-documented, yet fascinating history of the Marine Biological Laboratory, with briefer accounts of the sister laboratories at Woods Hole—those of the United States Fish Commission (successively the Bureau of Fisheries and the Fish and Wildlife Service) and the Oceanographic Institution. A background on the geography and early history of Woods Hole is first presented by Conklin. Then Lillie proceeds with a significant chapter on the origin of marine laboratories, including the dramatic story of Louis Agassiz at Penikese. Conklin recounts the establishment of the Fish Commission Laboratory and Lillie treats Alpheus Hyatt's seaside laboratory at Annisquam, which was most directly ancestral to the Marine Biological Laboratory. The relation of some good ladies of Boston to the Annisquam project and to the embryonic Woods Hole station is made clear: "The first step in the foundation of the Marine Biological Laboratory was taken by the Woman's Education Association in accordance with their decision to replace the Annisquam Laboratory by an independent and permanent station." Their generosity and far-sightedness is duly acknowledged, though it led to the domination of the first Board of Trustees by a group of Bostonians whose limited geographic view and rigid New England

economy came into sharp conflict with the broad and wise plans envisioned with apparent lack of practicality by the first director, C. O. Whitman. After a trying struggle, the administration of the laboratory was placed under the control of trustees elected by the corporation, which is made up of working biologists from various institutions over the country. Other crises were met, until the nation-wide, democratic organization became a set tradition.

The material growth of the laboratory into the world's greatest center of biological research is treated at length and in detail, fortunately by the man who long guided its development. The almost endless generosity of Charles R. Crane is of course extolled. The magnificent research record is summarized for the first twenty years only, but the dominating position of Woods Hole in the development of biology is amply indicated.

Brief but vivid pen sketches are given by Conklin and by Lillie of four of the dominating personalities of Woods Hole: Whitman, Crane, Drew and Gardiner. The two authors then let us feel the deep influence that the Woods Hole community life has had on the lives of the biologists and their families. Finally, a particularly valuable account is given of the foundation and functioning of the great Woods Hole Oceanographic Institution.

The unbounded enthusiasm and the warranted pride of the authors in the Marine Biological Laboratory left no room for qualifications. They say nothing of the relatively depauperate fauna of the North Atlantic; nothing of the restricted development of biology at Woods Hole, with increasing neglect of morphology, systematics, speciation, evolution, ecology, parasitology, fishery biology, and of many other still active branches of biology that do not emphasize the biochemical and biophysical aspects of the science; nothing of the narrowed view of biology which has thereby become installed in the minds of some scientists trained at Woods Hole. They say nothing of the limitations inherent in greatness, such as the inability

of newcomers to gain intimate contact with the masters; almost nothing of policies that have become fixed with age, for example, the limitation of instruction to four traditional courses; nothing of the failure of some Woods Hole habitués to make full use of research opportunities. Might not these limitations be recognized, without detracting greatly from our appreciation of the dominating role that this grand institution has continued to play in biological training and research? Perhaps a fresh consideration of these limitations might lead to even greater and broader progress.

The Skull of Sinanthropus pekinensis; a Comparative Study on a Primitive Hominid Skull. By FRANZ WEIDENREICH. Pehpei, Chungking: Geological Survey of China; New York: G. E. Stechert and Co. Paleontologia Sinica (New Ser. D) 10 (127), "1943" [1944]: i–xxxi, 1–486, pls. 1–93. $10.00 (paper).

THE discovery by Davidson Black of the very apelike hominid *Sinanthropus pekinensis* in a cave at Choukoutien, China, and the further description and interpretation of this missing link during the past two decades by Franz Weidenreich have been outstanding events in what may come to be known as the golden age of paleoanthropology. The extreme detail with which the relatively abundant remains of the "Peking Man" have been described and figured by Weidenreich in this and in preceding treatises should forestall such wasteful controversies as those that raged over the very similar *Pithecanthropus erectus,* largely as the result of the long-delayed and incomplete descriptions by Dubois. Whether or not other authorities will agree with Weidenreich in interpretations, they will all have full factual information.

Varied opinions on the phyletic position and nomenclature of this new fossil man have indeed already been expressed by experts. Some place it very low, others somewhat higher in the direct line of human ancestry, whereas still others regard it as an offshoot from some

primitive type. Some regard it as generically distinct from *Pithecanthropus* (the lack of the maxillary diastema may justify this view); others treat the two types as only specifically or even as only subspecifically distinct. All, however, must regard the discovery of *Sinanthropus* and the subsequent researches by Weidenreich as of paramount importance.

This last and most important publication on *Sinanthropus* is more than a very detailed osteological monograph—though that in the end may prove to be its most valuable feature. It includes an extensive comparison between the better known fossil types of man and a general discussion of their phylogeny.

The phylogeny of man is pictured as a very definite rectilinear sequence of stages which have evolved independently in different regions, as in China, the Indo-Australian Archipelago, Europe and Africa. Among known forms *Sinanthropus* and *Pithecanthropus* are regarded as nearest the anthropoid base of this hominid series, and the Neanderthalians are treated as transitional stages, along the several separate lines, between such ancestral types on the bottom and *Homo sapiens* on top. The evolution of man is held to have been a continuous process (or, rather, a completely parallel series of changes), wholly devoid of "chance variation" and of "real discontinuities." The calvaria is thought to have progressively lost its "superstructures" and to have become less massive and more glabellar, in inverse ratio to the degree of reduction of the face. It is admitted that there are some "disharmonies" within the "stages," but the possible association of a *Homo*-like cranium with an anthropoid type of mandible in the Piltdown Man is discarded as an artificial combination, as a chimera, and the association in *Pithecanthropus* of a *Sinanthropus*-like skull with a curved femur is held to be unacceptable. From the viewpoint of the principles of phylogeny, however, I see nothing unexpected or incongruous in such major differential combinations of archaic and progres-

sive features. Varied associations of characters seem to be the rule in involved phylogenies, particularly in those that have been complicated by reticulate evolution, as the human series seems to have been.

The transformation of the skull and face in human evolution is regarded as only a special case of a common evolutionary change. The domelike, thin-walled, brain-filled skull of man is paralleled by similar end structures in dwarf dogs and in the smaller species of various animal types. The concept of fetalization, however, is not mentioned in this connection.

In the scientific naming of the Hominidae Weidenreich violates the International Rules of Zoological Nomenclature as well as good systematic practice. For example, he quotes approvingly his earlier, unjustified renaming of *Homo soloensis* as *Homo primigenius asiaticus,* when he treated this form as a subspecies of Neanderthal man, but he promptly continues to call it *Homo soloensis.* An equally complex violation of the Rules is involved in giving the typical Neanderthal the preoccupied name, *H. p. europaeus. Sinanthropus* is held to represent almost the identical evolutionary stage as *Pithecanthropus,* in fact to be hardly more than racially distinct, yet the name *Sinanthropus* is maintained, because it would have been tactless for Black's successor to have eliminated the name! At least Dr. Weidenreich is frank in his flagrant disregard for the Rules and practices of zoological nomenclature.

The publication of this monumental treatise while the sponsoring nations are at war may receive some criticism at the moment but eventually will become a source of gratification and pride. The candle may be burning low, but it has not been extinguished.

The Mutants of Drosophila melanogaster. By CALVIN B. BRIDGES AND KATHERINE S. BREHME. Publ. Carnegie Inst. Wash., 552, 1944: i–vii, 1–257, pls. 1–3, figs. 1–128. $2.50 (paper), $3.00 (cloth).

THIS dictionary of the genetic structure of the genetically best-known annual species will produce in inter-

mittent Drosophila workers who are not now active with it an acute nostalgia which may easily turn them back to that field. For the constant devotees of Drosophila genetics it will be the ever-ready handbook, never far from the shelves of culture bottles, the binocular microscope and the record book. It puts in concise form, in a single scheme of arrangement, information of a type heretofore available only in scattered form in the seventeen volumes of Drosophila Information Service. The compilation of these data was carried on for many years by Dr. Bridges. Since his death, it has been completed and edited by Miss Brehme, working with Dr. M. Demerec. The important connection of Dr. Bridges with many phases of the evolution of Drosophila genetics is pointed out in a foreword by Professor T. H. Morgan.

The book starts with a short section on symbols of genes and names of characters, including occasional recommendation of one plan when several have been followed, and listing the precautions necessary for accurate crossover data. Then follows the major portion (226 pages) of the work, which is a list of the known mutations in *Drosophila melanogaster*, including many that have been lost or discarded. Information concerning each mutation is given under its symbol, and these are arranged alphabetically. Phenotype names are listed in the same alphabetic order, but the reference there is always to the symbol of the gene. Under this symbol are given the discoverer, date, locus in the chromosomes, references to the literature, a description of the phenotype, the source (whether spontaneous or induced) and other facts which will tell the investigator how useful the gene may be in any particular problem. There are 128 illustrations of mutations in this part.

Twenty-eight wild stocks, most of them still in existence in a few or many laboratories, are listed, with their peculiarities which constitute advantages or disadvantages. The linkage groups, omitting most lethals, are given in the order of their loci, so that one who looks for

neighboring genes finds them here, rather than in the alphabetic list. Each group is divided into two parts, one listing the most useful genes, the other those which would be used only in special situations. The small fourth group has a dozen mutations in it. Drawings of the external features of the fly, maps of its salivary gland chromosomes and a list of publications by Dr. Bridges complete the volume.

In its usefulness to a large and widespread group of investigators, this volume is comparable to the international tables in the physical sciences.

A. FRANKLIN SHULL

NOTICES OF NEW BOOKS

Mitosis. By FRANZ SCHRADER. Columbia Biological Series, No. 14. New York: Columbia University Press, 1944: i–x, 1–110. $2.00.—In this critical review mitosis, including meiosis, is treated from the physicochemical viewpoint. The whole emphasis is on the explanation of the mechanisms involved in nuclear division. The book is a "survey of past attempts to solve the puzzle that is mitosis. . . . Not one of the many hypotheses that have been broached has in it the definite promise of a final solution. But we have come to realize that mitosis is comprised of a great complex of different mechanisms." That would seem to constitute a good start toward a solution of a problem, the significance of which pervades all branches of biology.

The Peats of New Jersey and Their Utilization. By SELMAN A. WAKSMAN, H. SCHULHOFF, C. A. HICKMAN, T. C. CORDON and S. C. STEVENS. Bull. N. J. Agri. Exp. Sta. Rutgers Univ., 55 (pt. B), "1943" [= 1944] : 1–278, pls. 1–15, figs. 1–42.—This thorough, well-illustrated monograph carries much information that will be of value to ecologists and to students of Postglacial changes in floras and climates.

The Pacific World. Edited by FAIRFIELD OSBORN. New York: W. W. Norton & Co., 1944: 1–218, 28 maps and figs. $3.00.—Timely and sugar-coated, this little book will no doubt go far toward increasing knowledge of the Pacific half of the world. Stay-at-home Americans as well as many who are now in war service to the westward may learn from its pages essential facts regarding the great ocean, and its weather, islands, peoples and wildlife. The maps are of the pictorial type, and the whole presentation, though authoritative, reminds one of modernized museum exhibits.

Many Happy Days I've Squandered. By ARTHUR LOVERIDGE. New York and London: Harper & Brothers, 1944: i–xi, 1–278, 19 figs. $2.75.—Vivid accounts of a naturalist's adventures in Africa fill this book full of exciting reading. It contains also much first-hand natural history information, particularly on reptiles and mammals.

A New Manual for the Biology Laboratory. By BERNAL R. WEIMER and EARL L. CORE. New York: John Wiley and Sons, 1944: i–vii, 1–213, figs. A–G, 1–156 (many blank). $2.00.—This simplified laboratory guide supplements "Elements of Biology," recently prepared by Strausbaugh and Weimer. It is designed to aid the student in learning biological fundamentals through his own observation. Much of the text consists of thought-provoking questions.

General Zoology. By TRACY I. STORER. New York and London: McGraw-Hill Book Co., 1943 [1944]: i–xii, 1–798, many figs. $3.75.—The fact that this new text has already gone through four impressions attests its well-deserved reception. In the last printing a considerable number of small changes were made, assuring greater accuracy.

AMERICAN SOCIETY OF NATURALISTS

Secretary WILLIAM RANDOLPH TAYLOR announces the following new members of the American Society of Naturalists, elected as of 1943: Charles A. Berger, S.J., William C. Boyd, J. Gordon Carlson, Kenneth W. Cooper, C. W. Cotterman, R. W. Cumley, Lee R. Dice, Orie J. Eigsti, Ugo Fano, Adriance S. Foster, H. Bentley Glass, Myron Gordon, Ladley Husted, John S. Karling, Philip Levine, Walter E. Loomis, Ernst Mayr, Roland K. Meyer, Alfred E. Mirsky, Paul A. Moody, Orlando Park, Arthur W. Pollister, Harold W. Rickett, Herbert P. Riley, George D. Snell, Herman T. Spieth, Herluf H. Strandskov, Eileen Sutton, Johannes Van Overbeek and Alexander S. Wiener.

SHORTER ARTICLES AND DISCUSSION

CORPUS ALLATUM AND CORPUS CARDIACUM IN *CHIRONOMUS SP.*

HISTOLOGICAL studies on the endocrine glands of insect larvae have recently been reported from many laboratories. The glandular nature of the Corpus allatum and the Corpus cardiacum is a fairly well-established fact (Wigglesworth, 1934; Burtt, 1937; De Lerma, 1937; Pflugfelder, 1937). But in spite of these works, the histological changes of the above-mentioned endocrine glands during the whole life period of the animal have, so far as the authors are aware, been mostly neglected. The following observation is thus primarily concerned with these changes in the different developmental stages of *Chironomus sp.*

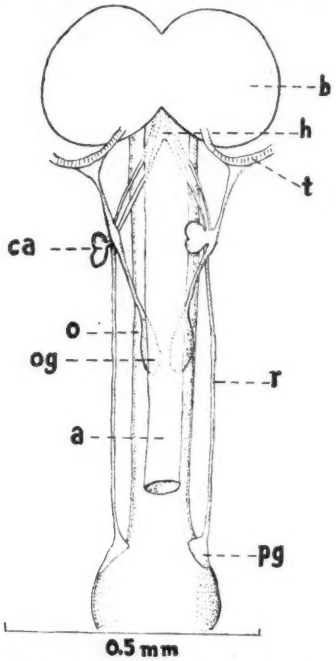

FIG. 1. Corpora allata and stomatogastric system of *Chironomus sp.* reproduced from Burtt. a, aorta; b, brain; ca, Corpus allatum; h, hypocerebral ganglion; o, esophagus; og, oesophageal ganglion; pg, stomachic ganglion; r, recurrent nerve; t, trachea.

Early in 1904, Holmgren recognized that the pair of small round bodies in Chironomus larvae were the Corpora allata, belonging to the stomatogastric nervous system. The system which

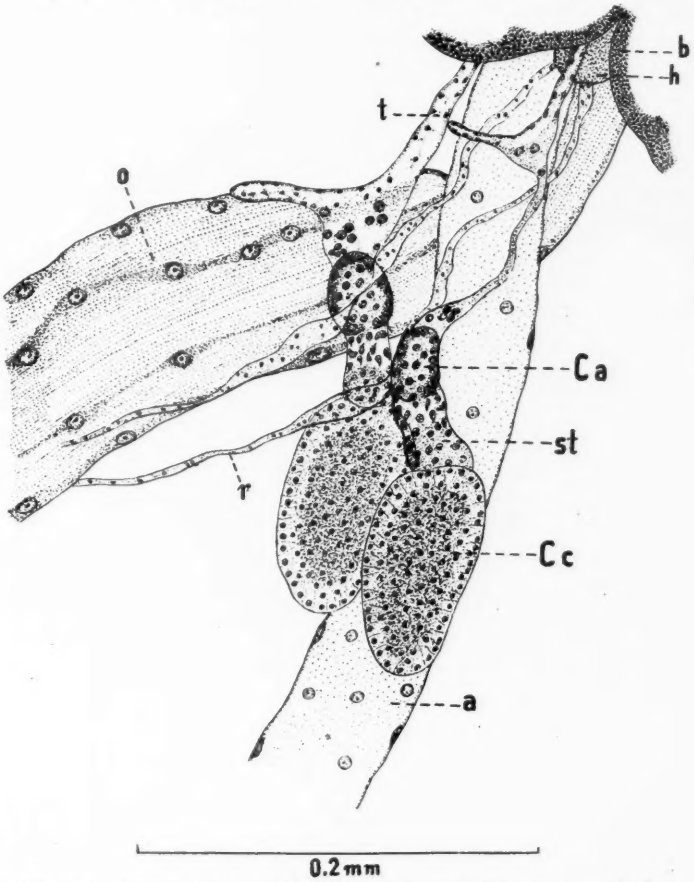

FIG. 2. Corpora allata and Corpora cardiaca of *Chironomus sp.* in last larval instar. In this and the following figures it represents the camera lucida drawing of total mount of the glands; fixed with Bouin and stained with borax-carmine. a, aorta; b, brain; C a, Corpus allatum; C c, Corpus cardiacum; h, hypocerebral ganglion; o, esophagus; r, recurrent nerve; s t, strand tissue; t, trachea.

has recently been studied by Burtt (1937) is reproduced here as Fig. 1. Fig. 2 is a camera lucida drawing from our own prepa-

ration. Despite their general similarity, our findings seem to differ from his in two respects. In the first place, it has been found that the Corpus allatum is imbedded in a strand of tissue which serves as a link between the trachea and the ellipsoid organ, and that they exhibit some conspicuous structural changes in the different developmental stages. Instead of a few cells, each of

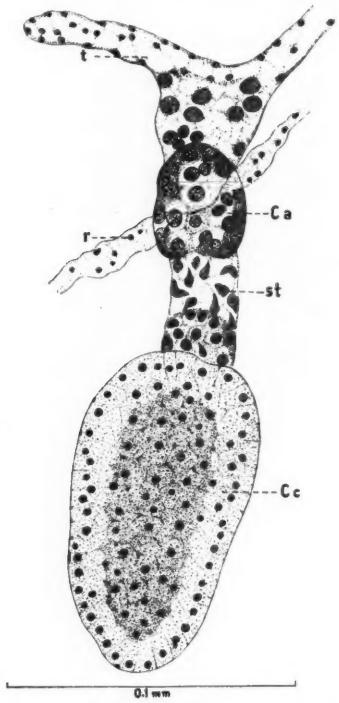

FIG. 3. Corpus allatum and Corpus cardiacum as represented in Fig. 2 magnified. The figure indicates the characteristic structures of the glands concerned in the last larval instar. C a, Corpus allatum; C c, Corpus cardiacum; r, recurrent nerve; s t, strand tissue; t, trachea.

them is composed of about 25 to 30 cells with nuclei of varying size in the last larval instar. Although there has been little doubt as to their glandular nature, we are quite unable as yet to decide whether the gland in question is the same gland as described by Burtt, owing to the fact that the latter did not mention which larval instar he had chosen. Secondly, the histological and the

anatomical features of the ellipsoid organs inform us that these bodies are really the Corpora cardiaca, which other authors sometimes call "oesophageal ganglia." As previously mentioned, the non-nervous structure of this endocrine gland has been made clear in the Orthoptera (De Lerma, 1937, and Pflugfelder, 1937).

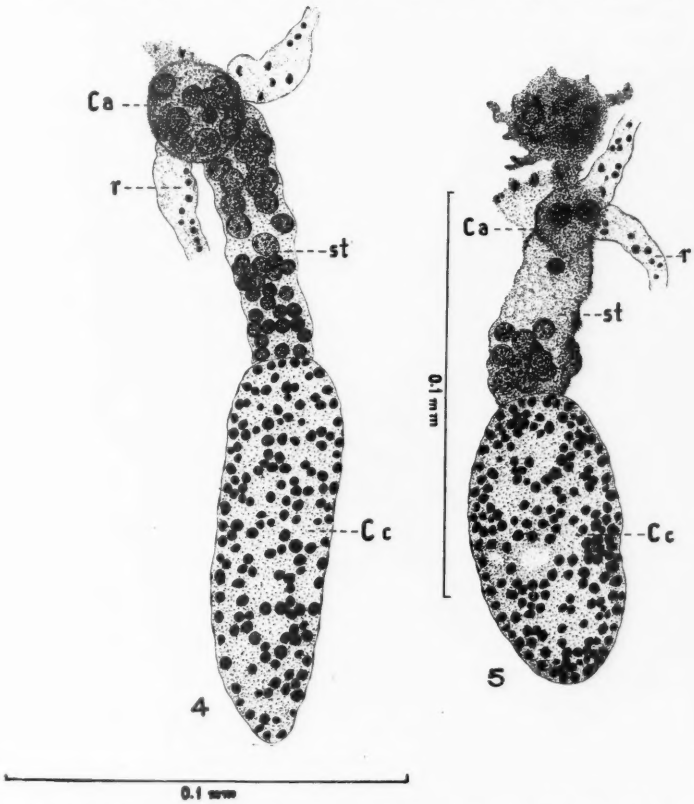

FIG. 4. Corpus allatum and Corpus cardiacum taken from a larva at the stage of thoracic swelling. The reduction in cell number and the size of Corpus allatum and the decrease in the distinctness of the cell boundaries and the size of Corpus cardiacum are all clearly shown. C a, Corpus allatum; C c, Corpus cardiacum; r, recurrent nerve; s t, strand tissue.

FIG. 5. Corpus allatum and Corpus cardiacum taken from a pupa at an early stage to show the degeneration of Corpus allatum and strand tissue, and the tendency of the nuclear pycnosis of the glandular cells of Corpus cardiacum. C a, corpus allatum; C c, Corpus cardiacum; r, recurrent nerve; s t, strand tissue.

For the present material, we are also unable to detect any nervous structure in these ellipsoid organs. So it seems more correct to call them Corpora cardiaca, instead of oesophageal ganglia. They are each composed of a great number of glandular cells. The observed changes of these two endocrine glands will now be given.

During the larval period, the increase in the body length of the larvae is accompanied by a corresponding increase in the size of Corpora allata. The glands, after having reached a mature condition, stop their growth in the last larval stage (Fig. 3).

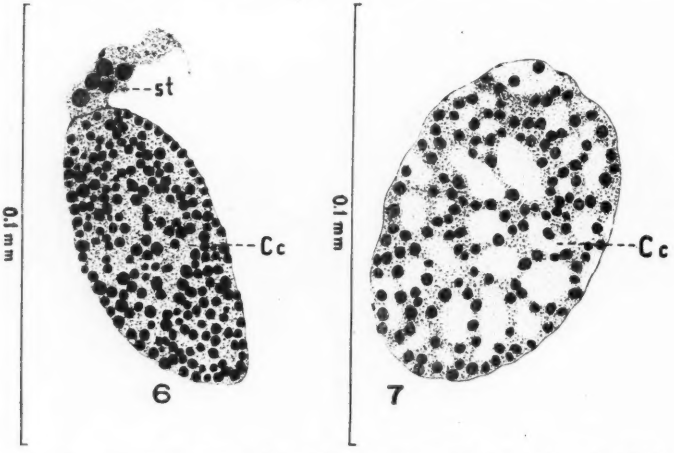

FIG. 6. Corpus cardiacum taken from a pupa at a later stage in which the Corpus allatum shows a complete atrophy and the strand tissue becomes very rudimentary. The nuclei of the glandular cells of Corpus cardiacum attained a highly pycnotic condition. C c, Corpus cardiacum; s t, strand tissue.

FIG. 7. Corpus cardiacum taken from an adult indicating a slight increase in the size of the gland. The strand tissue is no longer traceable at this stage. C c, Corpus cardiacum.

From this stage on, the larvae are now prepared to undergo pupation, as indicated by the characteristic enlargement of thoracic region (the stage of thoracic swelling). Then, the Corpus allatum begins to degenerate (Fig. 4). The degeneration process, characterized by the decrease in the distinctness of cell boundaries and the reduction of cell number (Figs. 4 and 5), leads to a complete atrophy of the gland later on (Fig. 6). In adults, the gland and its surrounding strand tissue are no longer traceable, as shown in Fig. 7.

Similarly, the Corpora cardiaca reach their maximum size in the last larval instar (Fig. 3). Their size then decreases gradually from the stage of thoracic swelling to the completion of pupation (Figs. 4–6), except, not infrequently, a slight increase in the adults (Fig. 7). The histological changes accompanying these form changes are: (1) The boundaries of individual glandular cells, which are clearly visible in the last larval instar, become indistinguishable at the onset of pupation; and (2) there is an increasing tendency for the condensation of nuclear materials from the stages of thoracic swelling onwards, so that in the pupa the gland is entirely provided with highly pycnotic nuclei. All these changes are clearly depicted in the figures.

Here then is the histological analysis of the Corpus allatum and Corpus cardiacum. The significant rôles played by them in the development of this insect, however, are not yet fully understood, owing to insufficient data. These will remain as problems for future investigation. From the existing evidence, it may safely be concluded that, at least for the material investigated, the Corpus allatum is a gland of holocrine type, while the Corpus cardiacum is definitely a merocrine gland.

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PARTIAL HERMAPHRODITISM AND DIGITAL ANOMALIES IN *NECTURUS MACULOSUS*

While conducting a laboratory in comparative anatomy certain abnormal individuals of *Necturus maculosus* were encountered that, in the opinion of the writer, were unusual enough to warrant special note and are here described.

The specimens concerned were purchased from the Biological Supply Company, Rochester, N. Y. Correspondence with that company revealed that these necturi were collected in Lake Winnebago, Wis., during the week preceding March 25, 1941.

In the collection were two males that were definitely abnormal. One specimen had a normal right testis with a greatly reduced left testis. By comparing a group of normal individuals it was determined that normal testes averaged 38.7 mm in length and 9.5 mm in width. In this first male, individual A, the reduced testis measured 13.0 mm in length and 2.5 mm in width. In all other respects this individual was normal.

The second male mentioned, individual B, had a normal right testis with dimensions of 35.5 mm in length and 12.0 mm in width, but instead of a testis on the left side there was a very poorly developed ovary. Normal ovaries of this lot measured 73.0 mm in length and 14.3 mm in width. The ovary of this individual measured 36.0 mm in length by 4.2 mm in width.

Critical examinations of this individual indicated that the Wolffian ducts on the two sides were not the same. The normal, right duct was of normal width and convoluted development, the average width of the duct was 1.5 mm. The Wolffian duct on the left side was not normally convoluted and was not as wide, 1.0 mm. The uriniferous tubules on the right side averaged 3 mm in length, while those on the left side were only 1.5 mm.

By removing the normal testis and comparing it histologically with a testis from a normal male it was found to be structurally normal. The gland on the left side, the vestigial ovary, clearly contained undeveloped ova. There was, however, no indication of a normal, female, functional Mullerian duct on the left side, thus preventing functional hermaphroditism.

The left fore foot of the same individual, individual B, possessed an extra phalanx extending from the side of digit number 3. By using the Alizarin red-staining and KOH-glycerine clearing technique the extra phalanx was clearly seen.

The right rear foot was very abnormal. Externally the foot appeared to have eight digits or two sets, one set superimposed over the other. By the Alizarin red, glycerine technique the double nature of the foot was clearly seen. There were six completely separate digits, metatarsals and phalanges. The fifth digits were fused at the base of the metatarsals. In addition to the abnormal digits it was seen that tarsal 2 was double with a separation of cartilages 4 and 5 into separate units.

Another specimen, individual C, possessed only three digits on the right fore foot. The Alizarin, glycerine technique indicated that digits 2 and 3 were fused at the distal ends of the corresponding metacarpals. The resulting digit contained only two phalanges, the normal number for digit 3.

The right rear foot of another specimen, individual D, possessed only three digits. By the Alizarin, glycerine technique it was determined that digit 4 was entirely absent. Either this digit had been lost or the fusion of digits 3 and 4 had been complete. Digit 5 on this same appendage contained only one phalanx instead of the normal two phalanges.

Discussion

In considering the variations in the digits described here it may be said that they are possibly due simply to irregularities in embryonic development. However, in view of the observations of Blaufuss (1941) on the venous variations in necturus collected from this same region, Oshkosh and Winnebago, Wis., these anomalies may be the result of environmental causes. Jenness (1942) reported variations in digit number in necturus, but made no mention of the locality from which the animals were collected.

Much has been written on hermaphroditism in the Anura, but so far as the writer is able to determine no description has been made of natural hermaphrodites in the Caudata. As Bayliff (1940) indicated in his discussion of an hermaphrodite in *Rana catesbiana*, it is the interpretation of many that such individuals represent cases of sexual reversal, probably from female to male phase.

The condition in which the Wolffian ducts were found in the hermaphrodite here described was what would be expected in view of the observations of Humphrey (1941) and Rodgers and Risley (1938). Rodgers and Risley noted that the accessory urogenital ducts were influenced, quite early in development, by the associated gonad. Humphrey artificially produced hermaphrodites in *Ambystoma* and observed that the effects of the implanted gonads on the secondary sexual characters depended upon the sex type of the gonad under whose influence their differentiation first occurred.

In the necturus described here the right mesonephric duct and accessory structures were definitely under the influence of the

normal testis found in connection with them. This duct on the left side was of the female type, logically under the influence of the ovary found there. However, the Mullerian duct on the left side was definitely of the male type, indicating the influence of the dominating testis. Also, the cloacal glands were of the male type, much swollen and highly glandular.

These observations seem to indicate that this animal did not represent an individual undergoing a sexual phase shift. Certainly if there was a phase shift in process here it was not from female to male which seems to be the usual type of shift reported for the Anura. The writer assumes that this individual presents an irregularity in development and not a shift in phases.

The probability is suggested that this individual represented one in which the bisexual state in development was persistent. Later in development the testis quite definitely assumed a permanent, dominating nature. As suggested above, such an irregularity may be the result of environmental factors of an undetermined nature.

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